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ECOLOGÍA DE LA DISPERSIÓN DE SEMILLAS POR PRIMATES DEL GÉNERO *Cebus* (CEBIDAE)

TESIS

QUE PRESENTA

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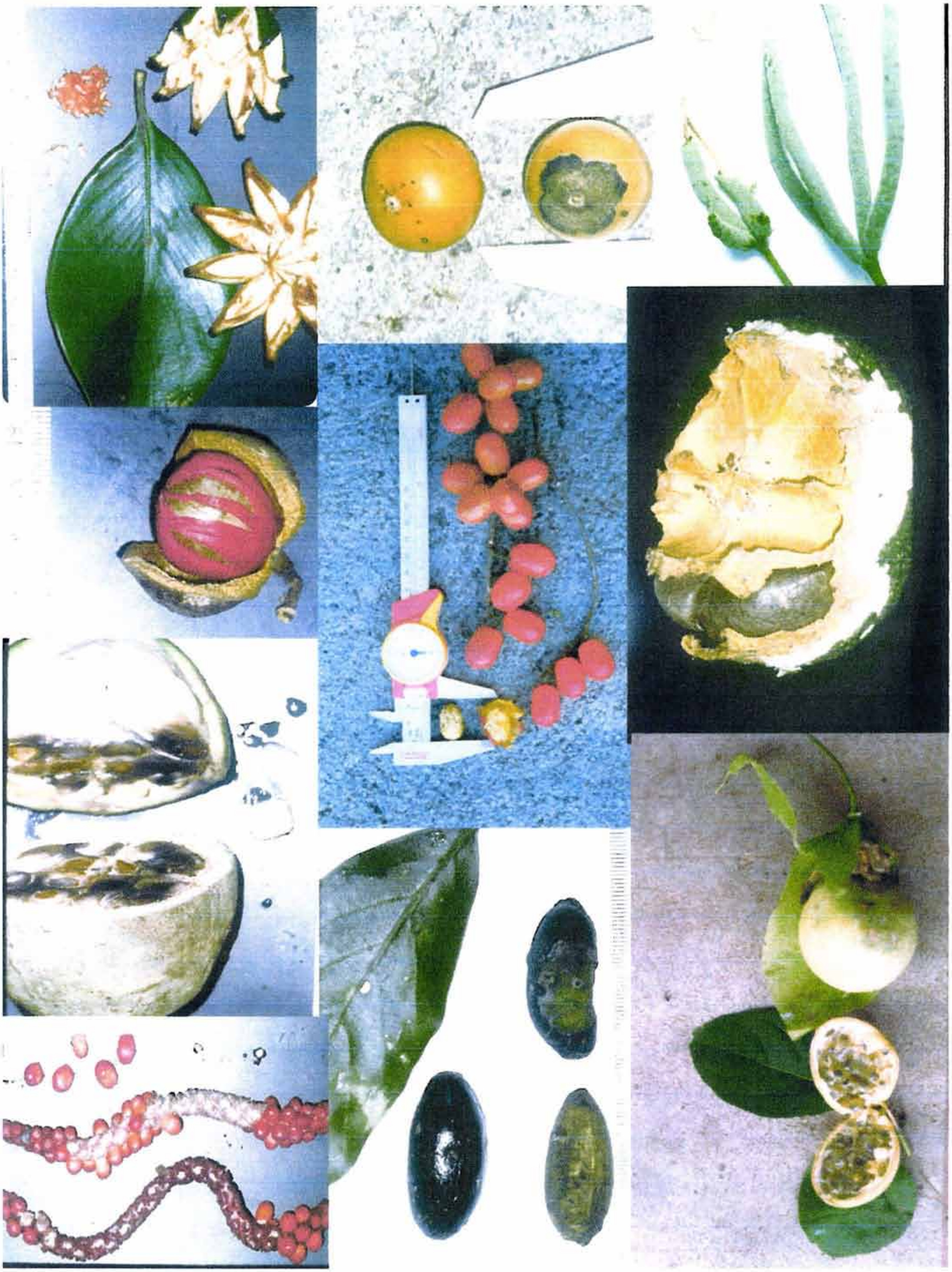

A mis padres, Rosa y Gerardo

"...porque hay en aquella tierra muy grandes pinares, y son tan grandes los pinos, que cuatro hombres juntos, tendidos los brazos, no pueden abrazar uno, y muy altos y derechos, y son muy buenos para mástiles de naos y para carracas, según su grandeza; las piñas son grandes, los piñones del tamaño de bellota..."

"Por aquella tierra hay muchos puercos monteses y monos que comen estos piñones de esta manera: que los monos se suben encima de los pinos y se asen de la cola, y con las manos y pies derruecan muchas piñas en el suelo, y cuando tienen derribada mucha cantidad, abajan a comerlos; y muchas veces acontece que los puercos monteses están aguardando que los monos derriben las piñas, y cuando las tienen derribadas, al tiempo que abajan los monos de los pinos a comellos salen los puercos contra ellos, y quítanselas, y comense los piñones, y mientras los puercos comían, los monos estaban dando grandes gritos sobre los árboles. También hay otras muchas frutas de diversas maneras y sabor, que dos veces en el año se dan."

De los trabajos que recebió en el camino el Gobernador y su gente, y la manera de los pinos y piñas de aquella tierra. CAPÍTULO VIII, COMENTARIOS DE ÁLVAR NÚÑEZ CABEZA DE VACA, Adelantado y Gobernador del Río de la Plata, (1555).

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DISCUSIÓN GENERAL

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RESUMEN

La dispersión de semillas es un proceso importante en el mantenimiento de los bosques ya que en general, al alejarse las semillas del progenitor tienen mayor probabilidad de supervivencia y establecimiento, incidiendo en el éxito reproductivo de las plantas y en la estructura de las poblaciones y las comunidades vegetales. Diversos son los agentes que intervienen en este proceso como por ejemplo los animales frugívoros. En este estudio investigamos el papel de un frugívoro "no estricto", monos del género *Cebus* (especie que complementa su dieta con frutos), como dispersor de semillas en tres tipos de bosques tropicales de América. Sus implicaciones en la demografía de plantas, evolución y dinámicas del bosque han sido subestimadas probablemente debido a su naturaleza generalista. Con este propósito, se efectuaron observaciones y experimentos que van desde estudios detallados en una especie de planta selecta, hasta estudios al nivel de la comunidad. Estos estudios se enfocaron en la evaluación de diferentes aspectos del proceso de dispersión de semillas por *Cebus*, enfatizando los referentes al componente de calidad de la dispersión. Los resultados obtenidos indicaron que *Cebus* tiene un papel activo en la dispersión de semillas, debido a que incluye una alta diversidad de frutos en su dieta; sus hábitos de forrajeo; la baja permanencia en los árboles de los que se alimenta; la dispersión de semillas a larga distancia; y principalmente el patrón de defecación que produce. Este patrón, a diferencia del que generan muchos frugívoros estrictos, se caracteriza por la alta probabilidad que tienen las semillas de ser dispersadas lejos de árboles conespecíficos, y compensa el reducido número de semillas por especie consumidas por los frugívoros no estrictos. En general, las tasas de remoción secundaria de semillas por otros organismos

fueron bajas y como consecuencia la mayoría de las heces de *Cebus* permanecieron por períodos prolongados sobre el suelo del bosque. Comparando dos especies de frugívoros no estrictos se observó que la cantidad pero no la identidad del material fecal afectó la actividad post-dispersión. Las semillas dispersadas en heces de manera esparcida tuvieron mayores probabilidades de supervivencia en el corto plazo que aquellas dispersadas de manera agregada. Además la mayoría de las especies de semillas consumidas fueron viables luego de ser defecadas y la germinación varió ampliamente entre los diferentes taxa de plantas. Bajas tasas de remoción de semillas de las heces de *Cebus* sumado a elevadas probabilidades de germinación sugieren una alta efectividad de la dispersión por *Cebus* y contrasta fuertemente con los patrones del destino post-dispersión de semillas en otras especies de primates. Este patrón es importante ya que el éxito de la dispersión no se ve limitado en comparación al generado por otros dispersores en la comunidad. La dispersión por *Cebus* a grandes distancias sugiere que las funciones de dispersión derivadas de los datos de trampas de semillas no describen adecuadamente los patrones generados por este primate. Por último, *Cebus* tiene importantes efectos en *Miconia*, una especie de planta pionera, dispersando sus semillas llevándolas a grandes distancias del origen. La frecuencia con la que ocurren estos eventos es de gran importancia biológica ya que favorecen la colonización de nuevos microhábitats y/o la homogenización de poblaciones de plantas. Por lo tanto, los estudios referentes a modelos de dispersión de semillas deberían considerar los patrones de dispersión a larga distancia producidos por vertebrados. En este estudio demostramos que los frugívoros no estrictos como *Cebus* juegan un papel importante como dispersores de semillas de un gran número de especies de plantas y en distintos tipos de bosques a lo largo de su rango de distribución.

ABSTRACT

Seed dispersal is an important process in the maintenance of forests. In general, seeds moved away from parental trees have higher survival and establishment probabilities, thus influencing the reproductive success of plants and the population structure as well as plant communities. Many agents are involved in this process such as frugivorous animals. In this study we investigate the role of a non-restricted frugivore, monkeys of the genus *Cebus* (a species that complements its diet with fruits), as seed disperser in three tropical forest types of America. Their implications in plant demography, evolution and forest dynamics have been underestimated probably due to its generalist habits. With this intention, we made several observations and experiments that ranged from detailed studies in a selected plant species to community level studies. These studies focused in the evaluation of different aspects of the seed dispersal process by *Cebus*, emphasizing those referred to the quality of the dispersal component. The results showed that *Cebus* plays an active role in seed dispersion because of a high fruit diversity diet; its foraging habits; the short time it spends on feeding trees; long-distance seed dispersal; and most importantly, the defecation pattern it generates. This pattern contrasts to those generated by many restricted frugivores, because of the high probability of seeds dispersed away from conespecific trees. It also balances the reduced number of seeds consumed per species by non-restricted frugivores. Commonly the secondary seed removal rates by other organisms were low thus most of *Cebus* faeces remained above the substrate for long periods of time. Comparing two non-restricted frugivores species we observed that it was the quantity but not the identity of the faecal material that affected post-dispersal activity. Scattered-dispersed seeds had higher

survival probabilities in the short term than the clumped-dispersed seeds. Additionally most consumed seed species appeared in viable conditions after defecation and their germination varied widely among the different plant taxa. Low seed removal rates from *Cebus* faeces in addition to high germination probabilities suggest high dispersal efficiency by *Cebus* and it markedly differs with post-dispersion seed fate patterns of other primate species. This pattern is important since the dispersal success is not limited in contrast to that generated by other dispersers in the community. Long-distance seed dispersal by *Cebus* suggests that the dispersal functions derived from seed traps data are not accurate in describing the patterns generated by this primate. Finally, *Cebus* has important effects on *Miconia*, a pioneer tree species, dispersing its seeds to long distances from the origin. The frequency in which these events occurre has great biological importance since it favors colonization of new microhabitats and/or homogeneization of plant populations. Therefore, studies on seed dispersal modelling should consider long-distance dispersal patterns produced by vertebrates. In this sutdy we demonstrate that non-restricted frugivores such as *Cebus*, play an important role as seed dispersers for many plant species and in the different types of forests along its distribution range.

INTRODUCCIÓN GENERAL

La frugivoría en sentido estricto se refiere al hábito que tienen muchos organismos de alimentarse de frutos que presentan estructuras carnosas. En sentido amplio se refiere a las consecuencias ecológicas y evolutivas que se derivan de esta interacción, tanto para los organismos frugívoros como para las plantas que producen estos frutos (Herrera 1982, Jordano 1992, 1995, Howe 1993, Martínez del Río y Restrepo 1993). Una consecuencia de la frugivoría es la dispersión de semillas. Ésta incide en el éxito reproductivo de las plantas y en la estructura y dinámica de las poblaciones y las comunidades vegetales (Dirzo y Domínguez 1986, Zhang y Wang 1995, Wenny 2000, Bleher y Böhning-Gaese 2001, Schupp *et al.* 2001). La dispersión de semillas es un proceso crítico para el mantenimiento de la diversidad de especies en los bosques tropicales (Estrada y Fleming 1986, Howe 1986, Fleming y Estrada 1993, Hubbell et al. 1999), ya que se ha demostrado que en muchos casos las semillas dispersadas lejos del árbol progenitor tienen mayores probabilidades de supervivencia y establecimiento que las que se quedan cerca de él (Janzen 1970, Connell 1971, Howe 1984, 1989, 1993, Harms et al. 2000). Esto se debe a que en general, los árboles en fructificación son focos de atracción de patógenos y depredadores debido a la gran acumulación de frutos y semillas en el vecindario de los mismos. A su vez, el establecimiento de un gran número de plántulas bajo la planta madre, produce un foco de atracción de diversos herbívoros. Así, los efectos negativos del vecindario en el reclutamiento de árboles resultan de un aumento del riesgo de mortalidad de semillas y plántulas debido a los patógenos (Burdon & Chilvers 1982, Augspurger 1983, 1984, Gilbert & De Steven 1996, Dalling *et al.* 1998, Packer & Clay 2000), los depredadores de semillas (Howe & Primack 1975, Janzen *et al.* 1976, Wright 1983, Clark & Clark 1984, Ramírez & Arroyo 1987, Forget 1993) y los herbívoros (Condit *et al.* 1992, Barone 1996, Coley & Barone 1996).

De esta manera la dispersión provee la oportunidad de escapar de los riesgos de mortalidad asociados con el vecindario de la planta madre y permite a las semillas colonizar nuevos ambientes que pueden ser potencialmente favorables para el establecimiento de las plántulas (Howe & Smallwood 1982). Esta acción puede ser llevada a cabo por distintos agentes como el agua, el viento y los animales frugívoros. Éstos juegan un papel muy importante dispersando las semillas a diferentes distancias de los árboles parentales (van der Pijl 1972). Sin embargo, la mayoría de los estudios han evaluado las curvas de dispersión de semillas a distancias cortas (unos pocos centímetros o metros) de las plantas parentales (Sauer 1988, Cain *et al.* 2000). Debido a la dificultad para medir los eventos de dispersión a larga distancia (Nathan y Mueller-Landau 2000) es poco común encontrar estudios que evalúen el extremo de la curva de dispersión (Portnoy y Willson 1993, Greene y Johnson 1995, Bullock y Clarke 2000, Fragoso *et al.* 2003). Sin embargo, estos eventos son los que probablemente tienen mayor significancia biológica en cuanto a ciertos rasgos de las poblaciones, como en la determinación de la estructura genética de las plantas a través del flujo génico a larga distancia, de las tasas de colonización de nuevos microhábitats y en la dinámica de metapoblaciones (Harper 1977, Sauer 1988, Hengeveld 1989, Hanski y Gilpin 1997, Hovestadt *et al.* 1999).

Puede esperarse que los animales frugívoros jueguen un papel muy importante en la dispersión de semillas a larga distancia. Existe evidencia acerca del efecto de los frugívoros en la dinámica poblacional de muchos árboles del trópico (Howe 1986, Chapman y Chapman 1996, Chapman y Onderdonk 1998, Wenny 2000, Bleher y Böhning-Gaese 2001, Poulsen et al. 2002, Fragoso *et al.* 2003) y en la contribución que realizan estos animales en el mantenimiento de la diversidad de especies arbóreas (Hubbell 1980, Howe 1993, Harms et. al 2000, Wehncke *et al.* 2003). En teoría, el conocimiento del comportamiento de los vertebrados frugívoros y las características de las plantas pueden combinarse para predecir los patrones de la dispersión de semillas a larga distancia y sus efectos en las poblaciones de plantas. Con el fin de entender el impacto que tiene un dispersor de semillas sobre una población de plantas, es útil evaluar los dos componentes de la efectividad de la dispersión: la cantidad y la calidad de la dispersión (Schupp 1993). La distancia a la cual un dispersor deposita las semillas está probablemente asociada al componente que tiene que ver con la calidad de la dispersión. El componente de cantidad está asociado con el número de semillas removidas y depende del número de visitas de los animales a los árboles con frutos, del tiempo de alimentación, de la cantidad de frutos/semillas disponibles y de la tasa de consumo (manipulación de frutos/semillas por frugívoro). El componente de calidad se define como la probabilidad de establecimiento que tiene una semilla una vez que es removida de la planta madre (Schupp 1993). Este componente depende del tratamiento que reciben las semillas cuando son manipuladas y consumidas por el frugívoro, de la calidad ambiental del sitio donde las semillas son depositadas y de los patrones de defecación de los dispersores (Lieberman y Lieberman 1986, Levey 1987, Zhang y Wang 1995, Andresen 2002, Wehncke *et al.* 2004). A su vez, el patrón de defecación está asociado al comportamiento y a los movimientos de los vertebrados frugívoros en espacio y tiempo, adquiriendo gran relevancia la distancia a la cual finalmente las semillas serán depositadas. Las especies de árboles que sufren mortalidad denso-dependiente o que dependen de claros para reclutar, se ven favorecidas por frugívoros que lleven sus semillas a largas distancias. Por medio de estos animales, la proporción de área que estas semillas pueden cubrir es mucho mayor que la proporción de área que cubrirían si no intervinieran estos frugívoros. Así, una mayor amplitud de dispersión está relacionada con: 1) una mayor proporción de reclutamiento de plántulas fuera del vecindario de la planta madre, 2) una mayor probabilidad de encontrar sitios seguros para el establecimiento, 3) una reducción del riesgo de mortalidad por patógenos y/o herbívoros, 4) una reducción del riesgo de competencia intra e interespecífica, 5) el flujo génico y la disminución de la probabilidad de "inbreeding".

La calidad de la dispersión que ofrecen diversos frugívoros es muy variable debido a la diversidad de vertebrados que consumen frutos (Bleher y Böhning-Gaese 2001, Poulsen et al. 2002, Fragoso *et al.* 2003). Por ejemplo, los vertebrados frugívoros difieren entre sí en cuanto a la proporción y el tipo de frutos que consumen y esta variación se ha utilizado para clasificarlos en dos grandes grupos: especies que se alimentan preferentemente de frutos, o sea, que dependen de una porción crítica de frutos en su dieta (frugívoros "especialistas") y especies que complementan su dieta con frutos (frugívoros "generalistas" o "facultativos" - ver Snow 1971, Morton 1973, y Howe 1993 para la definición de frugívoros "facultativos"). En este estudio nos referimos a los frugívoros "especialistas" como "estrictos" y a los "facultativos" como "no estrictos". Se ha postulado que las interacciones que poseen las plantas con uno u otro tipo de frugívoro tienen consecuencias ecológicas y evolutivas diferentes (Fig. 1) (Janzen 1970, Snow 1971, McKey 1975, Howe y Estabrook 1977, Howe y Smallwood 1982). Dado que la dieta de los frugívoros "estrictos" está compuesta por un alto porcentaje de frutos, es de suponerse que estos dispersen efectivamente las semillas que consumen y que muchos de los atributos de los frutos sean el resultado de las presiones de selección ejercidas por estos animales (Fleming et al. 1987, Russo 2003); (Fig. 1). Por otro lado, los frugívoros "no estrictos" consumen una gran variedad de alimentos como brotes, insectos, o vertebrados y complementan su dieta con frutos. Estos animales son menos constantes en las visitas a los árboles de una especie particular y se ha sugerido que efectivamente ejercen presiones de selección mucho más débiles sobre los atributos de los frutos (especies) que consumen (Fleming et al. 1993); (Fig. 1). Es posible, sin embargo, que los frugívoros "no estrictos" realicen también una dispersión efectiva de las semillas que consumen. Esto podría ocurrir si a pesar de remover pocas semillas de una especie particular, cada semilla dispersada obtuviese una probabilidad elevada de establecimiento (Fig. 2). Otro escenario probable sería que un frugívoro "estricto" removiera gran cantidad de semillas pero que fuera poco efectivo como dispersor al depositar las semillas de manera muy concentrada o en sitios desfavorables para la germinación y el establecimiento (Fig. 2). En ambos escenarios una alta calidad de la dispersión estaría relacionada tanto al arribo a sitios alejados de los árboles parentales, como también a sitios alejados de plantas conespecíficas, lo cual daría lugar a una alta probabilidad de establecimiento. Por lo tanto, una elevada calidad de la dispersión (*sensu* Schupp 1993) podría compensar e incluso elevar la eficacia de un frugívoro como dispersor (Fig. 2).

La calidad de la dispersión de semillas adquiere mayor o menor importancia dependiendo del grado de heterogeneidad ambiental (disponibilidad de sitios para establecerse) y del grado de presión de depredación que exista debajo de las copas de los árboles parentales. A lo largo de un continuo desde alta hasta baja presión de depredación bajo las copas de los árboles parentales como también de heterogeneidad ambiental podemos sugerir que la calidad de la dispersión de semillas adquiere mayor importancia cuando estas dos variables son elevadas. Su importancia disminuye a medida que nos acercamos al extremo en que ambas variables son bajas. Por lo tanto, en los bosques tropicales donde la heterogeneidad ambiental y la presión de depredación bajo de los árboles parentales son elevadas la calidad con la que las semillas son dispersadas es muy importante.

Los primates representan un sistema de estudio ideal para explorar el papel de los frugívoros "no estrictos" como dispersores de semillas ya que consumen los frutos de un elevado número de especies de árboles tropicales (Lieberman *et al.* 1979, Chivers y Hladik 1980, Estrada y Coates-Estrada 1984, Gautier-Hion *et al.* 1985, Garber 1986, Janson *et al.* 1986, Tuttin *et al.* 1991, Chapman 1995, Stevenson 2002). Los monos capuchinos (*Cebus* spp.) son considerados frugívoros "no estrictos" ya que, además de frutos, un porcentaje importante de su dieta está compuesto por insectos, vertebrados, huevos de aves y brotes tiernos. Diversos estudios basados en los distintos aspectos de su comportamiento, patrones de movimiento y uso de los recursos (Janson 1985, Chapman 1989, Mitchell 1989, Zhang y Wang 1995, Wehncke *et al.* 2003) han concluido que estos primates tienen un papel activo en la dispersión de semillas de muchas especies de plantas. Existen estudios que comparan la efectividad de la dispersión de semillas por un primate frugívoro "estricto" y uno "no estricto" (Zhang y Wang 1995). Estos autores reportan que *Ateles* (mono araña) dispersa muchas más semillas de *Ziziphus cinnamomum* (Rhamnaceae) que *Cebus* (capuchinos). Sin embargo, al evaluar la calidad de la dispersión se ha encontrado que las semillas consumidas por *Cebus* tuvieron 2.6 veces mayor sobrevivencia que aquellas consumidas por *Ateles*. Por lo tanto un frugívoro "no estricto" como *Cebus* puede tener un impacto importante en la sobrevivencia de las semillas dispersadas comparado con un frugívoro "estricto" como *Ateles*.

Con el fin de determinar si *Cebus* se comporta como un frugívoro no estricto en todo su ámbito de distribución y si genera un mismo patrón de dispersión de semillas en diferentes ambientes, en este estudio se han seleccionado tres bosques en los que se evaluó el papel de este género de primates como dispersores de semillas. *Cebus* se distribuye a lo largo de un amplio rango de ambientes tropicales, desde Honduras hasta el norte de Argentina (Wolfheim 1983).

El objetivo de esta tesis es determinar el papel de primates del género *Cebus* como dispersores de semillas y las consecuencias ecológicas de dicha dispersión (Figura 3). Este objetivo se abordó a través de estudios empíricos y experimentales que cubren desde detalles de la historia natural de una especie de planta selecta hasta estudios al nivel de la comunidad. Estos estudios están enfocados a evaluar diferentes aspectos del proceso de dispersión de semillas por monos del género *Cebus*, enfatizando principalmente los referentes al componente de la calidad de la dispersión (*sensu* Schupp 1993). La tesis se encuentra dividida en tres grandes secciones. La primera está enfocada a la descripción del proceso de dispersión por dos especies de monos del género *Cebus* (*C. apella* y *C. capucinus*) (Figura 3) en tres bosques tropicales y subtropicales de América (Argentina, Panamá y Costa Rica); (Figura 4). Se caracterizaron las distancias de dispersión y los patrones de defecación que produce *Cebus* en los tres bosques. Esta información fue generada para el mayor número de especies de plantas posible. Asimismo, con los resultados de este estudio se determina la importancia de los frutos en la dieta de *Cebus* en tres ambientes contrastantes a lo largo de su distribución y la generalidad del patrón de dispersión de semillas que producen.

La segunda sección de la tesis está enfocada a evaluar diferentes aspectos del componente de calidad de la dispersión asociados con el patrón de defecación de los monos del género *Cebus* incluyendo la manipulación de las semillas (ingestión y patrones de defecación), la comparación con otros frugívoros no estrictos y las posibles consecuencias del patrón de defecación sobre el mantenimiento de diferentes especies al nivel de la comunidad.

La tercera sección tiene como objetivo analizar en detalle el papel de *Cebus* como dispersor de las semillas de una especie en particular (*Miconia pussiliflora*). Este estudio complementa las observaciones y experimentos de las primeras dos secciones y ofrece información acerca de los eventos de dispersión a larga distancia producidos por este primate. Se estimó y comparó la lluvia de semillas de árboles focales con aquella producida por *Cebus*. Por medio de experimentos de germinación en el campo se evaluó el efecto de la dispersión por *Cebus* a diferentes distancias de los árboles maternos. Por último, por medio de un modelo de simulación espacial explícito, se evaluó la existencia y frecuencia con la cual ocurren los eventos de dispersión a larga distancia.

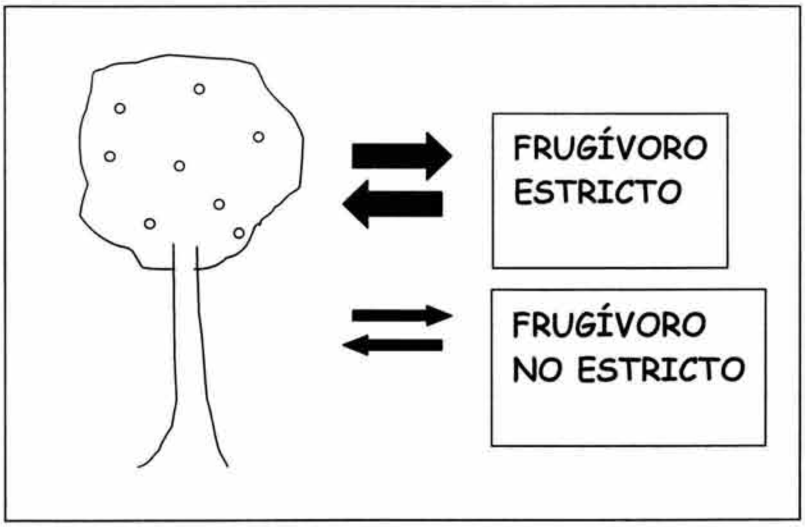

Figura 1. Representación gráfica de las consecuencias ecológicas y evolutivas derivadas de la interacción entre plantas y frugívoros. La dirección de las flechas indica la dirección de las presiones ecológicas y evolutivas de un organismo sobre otro. El grosor indica la intensidad de estas presiones.

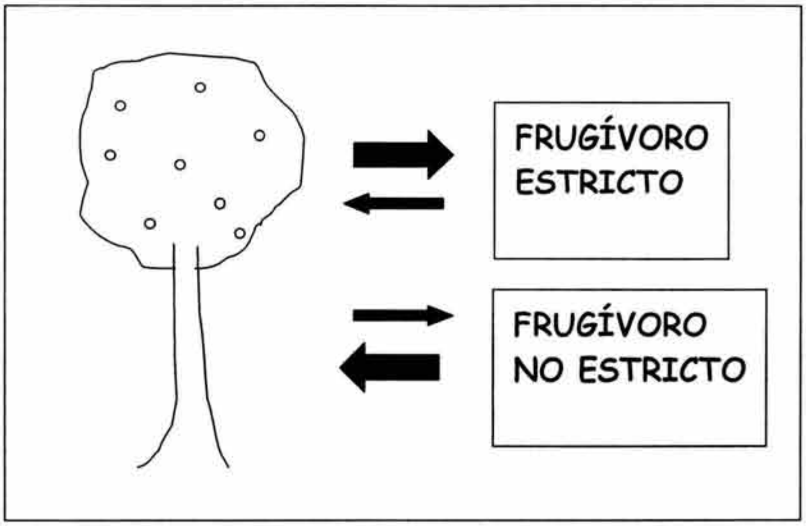

Figura 2. Representación de un posible escenario de las consecuencias ecológicas y evolutivas derivadas de la interacción entre plantas y frugívoros. La dirección de las flechas indica la dirección de las presiones ecológicas y evolutivas de un organismo sobre otro, y los grosores indican las intensidades de estas presiones.

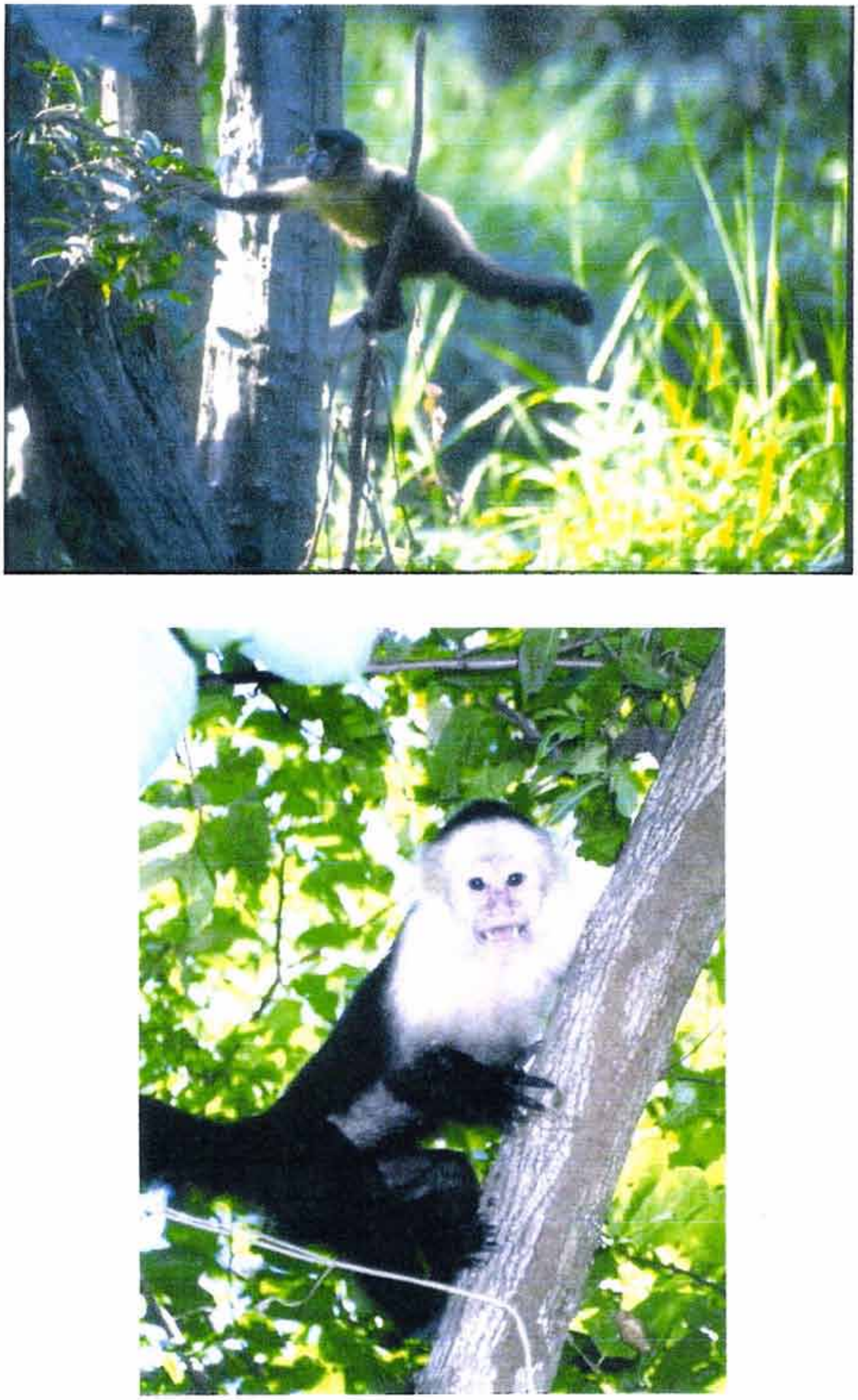

Figura 3. ARRIBA: Mono caí (*Cebus apella)*, ABAJO: Mono cara-blanca (*Cebus capucinus*).

Figura 4. Sitios de Estudio: Parque Nacional Palo Verde, Costa Rica (10°30'N, 85°30'W); Isla Barro Colorado, Panamá (9°09'N, 79°51'W); Parque Nacional Iguazú, Argentina (25°36'S, 34°34'W).

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CAPÍTULO I

El papel de un frugívoro no-estricto como dispersor de semillas en tres bosques neotropicales.

(Artículo en revisión en Ecography)

Patterns of frugivory and seed dispersal by *Cebus* monkeys along a geographical gradient

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Abstract

As the number of studies on seed dispersal by primates increases, a clearer picture of site specific effects emerges showing variations in the role that a single species may play depending on environmental factors. Here, we characterised different components of the diet and the dispersal process produced by monkeys of the genus *Cebus* in three contrasting forests of Central and South America. In each forest we evaluated diet selection, home-range, travel distance, and seed dispersal distance for *Cebus*. The three forests differed significantly in all the attributes considered of total fruits available. However, we found no evidence of diet selection by *Cebus* since the attributes of fruit consumed by *Cebus* did not differ from those of fruit available in each forest. Seed handling varied significantly between sites. Compared to Panama and Costa Rica few seeds were spit out or dropped in Argentina. We found no difference between sites in seed treatment. The evenness of fruit species consumed by *Cebus* was high and did not significantly differ between forests. The diversity of fruit species consumed varied according to the diversity of each site and was significantly lower in Argentina compared to Panama and Costa Rica. However, comparing the three forests, we found that *Cebus* swallowed a higher percentage of seed species of what was available in Argentina, the less diverse forest. In Argentina *Cebus* spent significantly more time feeding per fruiting tree and also travelled and dispersed seeds to significantly greater distances. For the three forests the highest probability of seed dispersal by *Cebus* fall between 100 and 400 meters from parent plants.Theory predicts that frugivorous specialists act consistently as effective seed dispersers, however, we show here that non-restricted frugivores like *Cebus* may also play an important role as seed dispersers, and we have probably underestimated their implications for plant demography, evolution and forest dynamics.

Introduction

Successful recruitment of trees in tropical forests depends on the effectiveness of seed dispersal (Howe and Smallwood 1982). The effectiveness of a disperser agent was defined by Schupp (1993) as the interaction of two components: the quantity (the number of seeds dispersed) and the quality (the probability that a dispersed seed will produce a reproductive adult) of dispersal. Frugivorous animals, and particularly primates, play an important role in this process (Janzen 1983) increasing the colonization probability of favourable sites by tree species and the opportunity to escape the neighbourhood of the parent plant (Howe and Smallwood 1982, Fragoso et al. 2003, Wehncke et al. 2003). Nonetheless, the role of frugivores as seed dispersers shows a large variation among and within species (see reviews in Chapman 1995, Zhang and Wang 1995, Sun et al. 1997, Chapman and Onderdonk 1998, Bleher and Böhning-Gaese 2001, Poulsen et al. 2002, Wehncke et al. 2004), which in turn produce heterogeneous selective regimes (Wheelwright and Orians 1982) that make fine-tuned reciprocal evolutionary change unlikely (Howe 1984, Herrera 1985, Russo 2003).

The effectiveness of primates as seed dispersers has been unclear since the first studies on this topic in the 1980's (see review by Stevenson 2002). Substantial evidence supports that primates may have a profound effect on the structure and diversity of the habitat where they live (Bourlière 1985, Chapman 1995, Chapman and Chapman 1995, Wehncke et al. 2003), because they have the potential to move seeds to new places (Chapman and Chapman 1995, Chapman and Onderdonk 1998). Many studies published in the last decade suggest that different species of primates may play dissimilar roles as seed dispersers derived mainly from their diverse feeding strategies and behaviours (see reviews in

Chapman 1995, Lambert and Garber 1998). Because diet and foraging behaviour determine the pattern of seed dispersal, a great variation in the effectiveness of dispersal between and within species of monkeys is expected. Such variation may also be influenced by the distribution and/or abundance of the food sources, the forest structure and diversity, and other essential elements like water and roosting sites (Terborgh 1983, Robinson 1986, Peres 1994). Yet, as the number of studies on seed dispersal by primates increases, a clearer picture of site specific effects emerges. There is evidence showing that the role played by a single species may vary depending on environmental factors such as seasonality and geographic location (Kaplin and Moermond 1998). The comparison of frugivory patterns and seed dispersal among populations of the same or closely related species, that share similar dietary requirements but live on different forest types, can increase our knowledge on the role of environmental variation in the effectiveness of seed dispersal by a particular species or guild. Capuchin monkeys (*Cebus* spp.) have similar feeding strategies which are characterized by a generalized diet based on fruits and arthropods. They are considered omnivorous, non-restricted frugivores (Chivers and Hladik 1980, Terborgh 1983, Janson et al. 1986, Robinson and Janson 1987), providing an excellent example of intermediate dietary adaptation and presumably effective seed dispersers (Zhang and Wang 1995, Wehncke et al. 2003, 2004).

The distribution of *Cebus* ranges from subtropical to tropical regions, thus allowing the assessment of frugivory and seed dispersal patterns of one "functional species" in a variety of contrasting forest habitats. Our aim here was to evaluate the different components of frugivory and seed dispersal by *Cebus* over a large geographical scale in neotropical forests. Specifically, our objectives were:

1. To evaluate how different components of the frugivorous habit of *Cebus* vary among three geographically separated forests that represent contrasting conditions of fruit diversity and environment (Barro Colorado Island, Panamá; Palo Verde National Park, Costa Rica; and Iguazú National Park, Argentina).
2. To evaluate how the seed dispersal patterns produced by *Cebus* vary among the three neotropical forests.

Methods

Study Areas

The study took place in three forests: one subtropical (Iguazú National Park, Argentina) and two tropical (Barro Colorado Island, Panamá; and Palo Verde National Park, Costa Rica). Of these three, Barro Colorado represents the forest with the highest species richness containing 1316 species of plants (Croat 1978). Palo Verde National Park holds 696 species (Chavarria et al. 2001), and the Iguazú National Park contains 106 species (Placci and Giorgis 1993). Barro Colorado (BCI) (9°10'N, 79°51'W) is a seasonally moist tropical forest of 1500 ha. About half of the island is young forest, mostly a hundred or more years old. The rest of the island has been covered with forest for about 400 yr. The flora and vegetation of BCI have been described by Croat (1978) and by Foster and Brokaw (1982). Average rainfall is 2600 mm with a seasonal dry period from January to April (Windsor 1990). The annual temperature averages 27 °C, with a mean diurnal variation of 9 °C. The main part of the study was carried out in old growth forest in the 50-ha Forest Dynamics Plot, on the central plateau of BCI. The plot is described in detail by Hubbell and Foster (1983) and Condit (1998).

Dr. Rafael Lucas Rodríguez Caballero National Wildlife Refuge, hereafter referred to by its popular name, Palo Verde National Park (10° 21' N, 85° 21 W), is located on the northern bank of the Tempisque River that forms the Gulf of Nicoya, Guanacaste Province, Costa Rica. It is about 7,550 ha large and includes several ecosystems such as tropical dry deciduous forest, interspersed with areas of secondary growth, grazed grasslands, riparian forest, seasonal swamp and marsh. Within the dry forest, trees vary in height reaching up to 20-25 m, with islands of evergreen vegetation distributed within deciduous and semi-deciduous areas. Elevations vary from approximately 3 m to over 200 m. The climate is characterized by a marked dry season from mid-December to the end of May. Mean annual rainfall is 1800 mm, with mean monthly rainfall during the dry season being as low as 15 mm. The site has been described in detail by Tosi (1969) and Vaughan et al. (1982).

The Iguazú National Park (25°40´S, 54°30´W) has a humid subtropical climate with marked seasonality in day length and temperature (Crespo 1982). It is about 60,000 ha and is dominated by secondary forest. Annual rainfall in the area averages 2000 mm (Brown and Zunino 1990). The winter season (June-August) is characterized by both a lower production of fleshy fruits and lower availability of arthropods than spring and summer seasons (October-March) (Placci et al. 1994, Di Bitetti 2001). The size of study area used in each of the three forests was of approximately 150 ha.

The fauna, flora, vegetation structure, phenology, seasonality, and rainfall and temperature regimes of the three forests are different. Therefore, in order to be able to compare the results of these sites we selected the period of higher fruit availability in each forest. Because it was impossible to study the three forests at the same time, we sampled Iguazú in November-December 1997 and during two periods in 1998 (February-March, September-October). Data from BCI were collected in March-July 1999, while those from

Palo Verde in July-August 1999 and April-June 2000. Although these data are not strictly comparable, they allowed us to describe the most salient characteristics of the role of *Cebus* as seed disperser in each site.

Study species

The tufted or brown capuchin monkey *Cebus apella* is the only monkey species inhabiting the Iguazú National Park. It occupies a variety of habitats in tropical and subtropical forests throughout much of South America, from Colombia to northern Argentina. On BCI, the white-faced monkey, *Cebus capucinus* lives in sympatry with other four species of monkeys: howler monkeys (*Alouatta palliata*), tamarins (*Saguinus geoffroyi*), night monkeys (*Aotus trivirgatus*), and a single re-introduced group of spider monkeys (*Ateles geoffroyi*). In Palo Verde, Costa Rica, *C. capucinus* lives in simpatry with howler monkeys and spider monkeys (Freese 1976). Like brown capuchins, white-faced monkeys have an extensive distribution ranging from Honduras to Ecuador (Wolfheim 1983).

Although we studied two different species of *Cebus* we considered them as one "functional species". This is based on the fact that *Cebus* have similar dietary requirements. *Cebus* is an omnivorous species with a diet based on fruits and arthropods, but it also consumes vertebrates, shoots, and bird eggs (Oppenheimer 1968, Terborgh 1983, Milton 1984, Moscow and Vaughan 1987, Robinson and Janson 1987, Mitchell 1989, Brown and Zunino 1990). Brown capuchins spend 70-90% of their day time harvesting food, and some studies report that they spend more time looking for insects than feeding on fruits (Terborgh 1983, Robinson and Janson 1987). At Iguazú National Park, Di Bitetti (2001) reported that brown capuchins consume fleshy fruits from at least 81 different species of trees, vines, shrubs and epiphytes, and that food abundance and distribution is the main determinant of their home-range. Previous work on BCI has shown that the bulk of white-faced diet (65%) is made up of fruits and that group movements are related to the location of fruit sources (Hladik and Hladik 1969, Mitchell 1989). Brown capuchin adults weigh *ca.* 2.2-3.6 kg (Robinson and Janson 1987). In Argentina, they live in multi-male and multi-female polygamous groups ranging from 7-30 individuals. White-faced monkeys weigh on average 3 kg (Milton 1984) and also live in permanent social groups ranging from 5 to 24 individuals in BCI (Oppenheimer 1968, Mitchell 1989), and from 15 to 23 individuals in Palo Verde (Massey 1987, Moscow and Vaughan 1987). At least 16 groups with an estimated population of 278-313 individuals live in BCI (Mitchell 1989). Groups at Palo Verde vary in size with overall mean densities of 15 individuals/km^2 (Massey 1987). In comparison with other species of monkeys both, brown and white-faced capuchins showed (i) short feeding bouts per tree and removal of most ingested seeds away from the source tree; (ii) long-distance and near-continuous daily movement patterns; (iii) scattered deposition of seeds through frequent defecations; (iv) inferred low rates of post-dispersal seed predation; and (v) gentle treatment of swallowed seeds (Wehncke et al. 2003, 2004, Wehncke and Dalling in press, Wehncke pers. obs.).

Data collection

Diet and feeding patterns

In each site the composition of *Cebus* diet was compiled by direct observations of feeding events and from collection and analyses of the faecal material. We identified the species of fruit eaten by collecting a sample of the fruit, seed or other plant part. Additionally, we registered how seeds were handled by the monkeys by assigning seed treatment to one of three broad categories (seeds spat out, dropped and/or swallowed). By analyzing the faecal material we registered the condition of seeds after passing through the gut of the monkeys (intact or destroyed). When available, we sort 10-40 seeds of every faecal sample to evaluate viability by germination experiments. We identified at the species or at least at the genus level and counted all seeds in faecal samples. Feeding bouts per tree were calculated with estimations of the time elapsed between the arriving (the time when the first member of the core group, non-peripheral subordinate individuals, started feeding) and departure (the time when the last member of the group finished feeding) of the group from a feeding tree (see Wehncke et al. 2003).

To have an estimation of the importance of fruits in *Cebus* diet in each site we calculated the percentage of fruit species consumed from what was available during the corresponding study period. From several sources of information (J. Wright, R. Perez, R. Foster, unpublished data; Placci et al. 1994; Chavarría et al. 2001) we estimated the number of plant species fruiting during the study period per site. These included vines, lianas, epiphytes and trees with fleshy and dry fruits known or potentially eaten by *Cebus*.

In order to evaluate which fruit attributes were used by monkeys during their foraging activities, we estimated the availability of fruits in each of six categories in every site. We considered the following fruit attributes: fruit type (achene, aggregate, berry, capsule, drupe, follicle, legume, nut, monocarp, syconnium and syncarp); fruit size diameter (small = < 1 cm, medium = 2-3 cm, large = > 3 cm); aril (presence or absence); number of seeds per fruit (1, 2-5, 6-20, > 20 seeds per fruit); seed size (small = ≤ 0.5 cm, medium = > 0.5 < 2 cm, large = ≥ 2 cm); and fruit colour (black-purple, brown, green, orange, red, white and yellow). We further assessed the number of instances in which monkeys consumed fruits of each category (consumption). These data were then analyzed by means of a logistic model with nominal response (SAS Institute 1988). This analysis produces a Likelihood-Ratio test that approximates to a Chi-square test. We performed separate analyses for each fruit attribute. Each model included site and fruit consumption as main factors. A significant effect of site would be indicative of differences in the distribution of a given fruit trait among sites. Consumption evaluates if there is a general difference in the trait distribution between the available and consumed fruits. Finally, the interaction term assess if diet selection occurs in some sites but not in others.

Seed handling (swallowed, dropped and spat out) and seed treatments (intact, destroyed, and not passed through the gut of monkeys) of the fruits consumed by *Cebus* were analyzed among sites using contingency analyses.

In order to quantitatively determine the diversity of *Cebus* diet and whether they consume fruit species more or less evenly in each forest, we calculated the Shannon diversity (H') and the evenness (E) indices of the fruit species used by these monkeys (Magurran 1988). In each site, the total number of individual plants per species and the total number of plant species used by the monkeys were compiled by observational data and by the presence of fruits in the fecal sample collection. The values of the Shannon diversity index commonly fall between 1.5 and 3.5 (Magurran 1988). We used the program Species diversity and richness (vers. 1.2, 1997) to calculate H' and E indices with their corresponding 95% confidence limits. The procedure performed a randomization test and recalculated each index with 10,000 random partitions. Differences in diversity and evenness indices between sites were evaluated using the same program.

To evaluate the consumption pattern in relation to the number of species available at each study period and site, we estimated the percentages of species manipulated, ingested and swallowed from the total number of species available. Species manipulated refers to all the species handled by the monkeys either for insects or any other plant part consumption. Species consumed refers to species whose fruits were eaten but seeds were not swallowed; and species swallowed were only those which seeds were swallowed. In each forest we measured the time spent feeding per fruiting tree and the percentage of observation time feeding on fruits. We used the Chi squared test to evaluate differences among the three forests.

Ranging and seed dispersal patterns

We hypothesized that the role of disperser species may vary depending on environmental factors and forest type (Terborgh 1983, Robinson 1986, Zhang 1995, Di Bitetti 2001). Hence, we compared three variables associated with the movements of monkeys that potentially affect the dispersal process: home-ranges use, travel distance, and seed dispersal distance, which were determined through following groups of individuals.

The number of individuals followed in each site was approximately the same. In Iguazú we followed one group of 30 individuals of brown capuchins; in BCI we followed two groups of white-faced monkeys of 15 and 17 individuals each; and two groups of 16 and 22 individuals in Palo Verde. In all sites monkeys were followed from dawn to dusk, and observations were more or less evenly distributed across all hours of the day. Individual animals were recognized by their physical features which allowed us to track the same group. Home range size was described by plotting the location of the group every 10 minutes or when changes in the direction of travel occurred. We used compass and pedometer to register locations from trails. In Iguazú, a network of trails was established covering an area of *ca.* 6 km^2 marked at 50 m intervals by flagging indicating trail name and distance. On BCI, locations were determined by recording the tag number of the closest tree inside the 50-ha Forest Dynamics Plot located on the central plateau. Outside the plot, locations were estimated also using compass and pedometer. In Palo Verde, all the locations were estimated by using a GPS (Garmin 12), compass and pedometer. We evaluated if distances travelled per hour differed between sites using the Kruskal-Wallis test.

The daily distances travelled by the troops, the position of all trees used as food sources, the locations where defecations were deposited, and the average time of passage of seeds through the guts of monkeys were used to estimate mean seed dispersal distances. Mean seed retention times in *Cebus* digestive tracts (1.40 h) were obtained from studies with captive monkeys (*C. capucinus*, Wehncke et al. 2003; and *C. apella*, E.V. Wehncke unpublished data). We considered in the analyses trees in which monkeys spent more than 5 min feeding on fruits and those that have seed sizes that fall in the range of swallowed seeds. Estimations were obtained by measuring the distance between the source tree and the position of the group at the moment of defecation directly on maps. Based on these data we calculated the probabilities of seed dispersal for the three sites of study.

To describe the pattern of range use by the monkeys we estimated the 'utilization distribution' of monkey`s home range. The utilization distribution describes the amount of time that an animal spends in any place of its range (Seaman and Powell 1996). Using this model, range size is described in terms of its use, and it is defined as the minimum area in which an animal has some specified probability to be encountered (Worton 1995). For our analyses we used the probabilistic Kernel method (see Wehncke et al. 2003), which is particularly useful for analysis of non-normally distributed data, as is the case for most tracking data. Finally, we selected the Kernel method because we were interested more to analyze tracking data with respect to range use patterns (identification of foraging areas) than for the calculation of range size. Due to the autocorrelated nature of our data, sizes of foraging areas calculated with the Kernel method were not compared statistically.

Results

Diet and defecation patterns

Pooling the data from the three forests (n = 148 species of fruit), it was apparent that *Cebus* consumed fruits without aril (88%). They consumed more berries (29%), drupes (28%) and capsules (21%) than any other fruit type. Considering fruit colours and sizes they consumed black-purple (22%), red (20%) and brown (17%) fruits of medium (44%) to large (37%) size. Most of these fruits contain 1 (34%) or more than 20 seeds (37%) of small (42%) to medium (41%) seed size.

Logistic analyses showed that excepting fruit type, the distribution of all other fruit attributes differed among sites (Table 1). There were no significant differences in fruit consumption for any attribute, indicating that monkeys did not select fruits on the basis of the measured traits (Table 1). As indicated by the lack of significance of the interaction terms, the lack of fruit selection is consistent among the different sites.

The Chi square contingency analysis demonstrated that seed handling (χ^2 = 10.2, df = 4, P = 0.04) but not seed treatment (χ^2 = 5.7, df = 4, P = 0.2), significantly differed among sites. Although in all sites monkeys swallowed most of the seeds they handled (from 67% to 92% of seeds handled), in Panama and Costa Rica they spit (14% and 18%, respectively) and dropped seeds (20% and 4%, respectively) more frequently than in Argentina (spit 8% of seeds handled, no seed were dropped).

Results from faecal analyses showed that in all study sites a high percentage of the faecal samples collected contained intact seeds. In Panama 93% of the faecal samples (n = 174) contained seeds, 98% (n = 162) in Costa Rica and 88% (n = 48) in Argentina.

The diversity of diet followed the decreasing pattern of plant diversity from Panama to Costa Rica and then to Argentina (Fig. 1). *Cebus* consumed fruits of more tree species in Panama (75 species) than in Costa Rica (23 species) and Argentina (14 species). The Shannon diversity index of fruit species that composed the diet of *Cebus* was not significantly different between Panama (H' = 3.3, n = 71 species) and Costa Rica (H' = 2.8, n = 21 species); (P = 0.17), but both sites showed significant differences with Argentina (H' = 2.02, n = 14 species); (Panama: P < 0.0001, and Costa Rica: P = 0.0001). Monkeys consumed fruits of different species evenly in all sites (Fig. 1), with no significant differences between sites (P = 0.18).

Cebus manipulated more fruit species in Panama (105 species), than in Costa Rica (30 species), and Argentina (14 species). When we estimated the percentage of species manipulated, ingested, and swallowed from the total number of species available at each study period and site, we found that Costa Rica and Argentina showed the highest values (Total number of species available: 23_{IGZ}, 240_{BCI}, 37_{PV}), (Fig. 2).

The time the monkeys spent feeding in each fruiting tree varied significantly between the three forests ($\chi^2 = 99.3$, df = 2, $P < 0.0001$). Monkeys spent more time feeding per tree in Argentina than in Panama and Costa Rica (Fig. 3). When we evaluated the time spent feeding on fruits in relation to total observation time, we found the same decreasing trend from Argentina to Costa Rica and Panama. *Cebus* spent 57% of observation time feeding on fruits in Argentina, 53% in Panama, and 31% in Costa Rica (Fig. 3).

Ranging and seed dispersal patterns

There were significant differences between sites in distances travelled per hour by *Cebus* (Kruskal-Wallis test, $\chi^2 = 38.8$, df = 2, $P < 0.0001$), with *Cebus* travelling greater distances in Argentina (n = 22, n = 58, n = 22, for BCI, Iguazú and Palo Verde, respectively) (Fig. 4). Accordingly, seed dispersal distance also differed between sites (Kruskal-Wallis test, $\chi^2 = 61.6$, df = 2, $P < 0.0001$) and had the same trend of decrease from Argentina to Panama and Costa Rica (Fig. 4). For the three sites of study the highest seed dispersal probability fell approximately between 100 and 400 meters from parent plants (Fig. 5). Home range used also decreased from Argentina (172 ha) to Panamá (150 ha) and Costa Rica (70 ha).

Discussion

Diet and defecation patterns

Cebus monkeys showed no selection on fruit characteristics in any of the three forests studied, suggesting that monkeys consumed from what was available at each site. In addition to the omnivorous diet of *Cebus* reported on several studies (Terborgh 1983, Robinson and Janson 1987, Brown and Zunino 1990, Di Bitetti 2001), here we showed that this lack of selection extends to fruit traits.

Seed handling and further seed treatment in the gut are also important characteristics of the quality component of seed dispersal. *Cebus* exerted a gentle treatment of swallowed seeds, leaving most of them in viable conditions. Seeds were similarly treated in the gut of monkeys irrespective of the site. This is not surprising since the transit time of seeds through *Cebus* gut is independent of seed size (Wehncke et al. 2003), and therefore seed treatment may be more associated to the physiology of *Cebus* than to seed traits. According to Wehncke and Dalling (*in press*) endozoochoria by *Cebus* does not have a consistent effect on seed germination, since it may benefit some species while harming others. In contrast, seed handling differed among the three forests. We suggest that this result may be more associated with differences in the time spent feeding per fruiting tree between sites, the generalized diet of these monkeys, and with characteristic of the forest type, than to fruit and seed traits. However, we cannot be sure about this last statement. In all sites monkeys swallowed most of the seeds they handled, however, in Panama and Costa Rica they spit out and dropped seeds more frequently than in Argentina. This may also be a consequence of the time spent feeding per fruiting tree and may have consequences in the fate of those seeds. Seeds that are swallowed can travel further distances having the potential advantage to colonize new microhabitats.

Cebus manipulated and consumed a higher diversity of fruits in Panama and Costa Rica than in Argentina. We also found that the evenness with which fruits were used was high in the three environments, suggesting that species were represented more or less equitatively in the *Cebus* diet. Argentina, followed by Costa Rica and Panama, showed the highest values in the percentage of species manipulated, consumed, and seed species swallowed relative to the total species available that could be potentially consumed by monkeys, in the corresponding period. This suggests that in each site *Cebus* consumed according to what is offered. In Argentina, they spent more time feeding on trees than at the other two sites. Since the time spent per fruiting trees is much less than the seed transit time through the gut of *Cebus* (Wehncke et al. 2003), the occasions when monkeys do not move and remain on trees may have no severe consequences for the seed dispersal pattern.

Ranging and seed dispersal patterns

The longer distances travelled per hour and the higher seed dispersal distances produced by *Cebus* in Argentina could be explained by factors such as the low risk of predation and the shifting use of different parts of the home range tracking resources that are heterogeneously distributed in space and time. Another factor could be the larger group size of *Cebus* in Argentina when compared to the other two sites (Di Bitetti 2001). A positive relationship exists between group and home-range use, which is similar to that observed between body size and home-range size in mammals, with larger mammals having greater home-ranges. Other plausible explanations for the long dispersal distances observed in Argentina may be the relative low availability of fruit sources that results in a need to travel longer distances. The increment in day length (that corresponded with the period of study) may be another possible cause of the longer distances registered. Several factors such as the availability of water holes during the dry season, the availability and distribution of sleeping trees, predation risks, the distribution of food sources other than fruit (vertebrates and invertebrates), and inter-group relationships may affect the movements and the home-range size of *Cebus* (Terborgh 1983, Robinson 1986, Zhang 1995, Di Bitetti 2001). Since this study took place in different environments, and with different composition of primate species, we should be cautious about drawing global conclusions. However, we may suggest possible explanations to the general patterns observed from the comparison along the geographical gradient considered.

Several studies have supported that one characteristic shared by the different *Cebus* species is that fruit abundance and distribution seem to be the main determinant of home-range use (Hladik and Hladik 1969, Mitchell 1989, Janson and Di Bitetti 1997, Di Bitetti 2001). This is evidenced by the shifting pattern of use related to the distribution of their main fruit sources and by the increase in home-range size during periods of fruit scarcity (Di Bitetti 2001). However, one study in Panama (Wehncke et al. 2003) found no clear evidence that *Cebus* monkeys move in relation to the location of preferred available fruit sources. Given the high diet breadth of this primate in Panama, we would expect the distribution of reproductive trees to have only a relatively diffuse effect on foraging locations during the period when most plant species fruit. However, the combination of other characteristics like the short feeding bouts per tree, the relatively high proportion of fruit available and some variation in the spatial location of fruiting trees may result in shorter dispersal distances in Panama compared with those of Argentina. Unfortunately, we do not have precise information on the distribution of reproductive trees within the home range of *Cebus* in Costa Rica to estimate whether their movements follow the spatial location of resources. However, here we reported low values of travel distance and of seed dispersal distances by *Cebus*. As Terborgh (1983) suggested, a factor that could explain a concentrated use of the home-range by monkeys is the regular use of one essential element in short supply, such as water holes. Costa Rica was the driest forest compared to the other sites; therefore, though not analyzed here, the distribution of water holes might help to explain the short travel distances reported for this forest.

Cebus consumed fruits according to what was available in each forest type. This generalized pattern agreed with the diversity and evenness with which they consumed fruits among sites and with the time spent eating at each fruiting tree, which in turn varied according to the fruiting species diversity of each site. Different contexts of diversity determine different patterns of foraging thus influencing monkey's movements, and consequently, seed dispersal distances. Thus, we predict that non-restricted frugivores like *Cebus* may play an important role as seed dispersers, and we have probably underestimated their implications for plant demography, evolution and forest dynamics. However, we should be careful in establishing a causal relationship between the differences of diversity contexts, the pattern of frugivory by *Cebus* and the differences in seed dispersal, since several other factors like differences in potential predators, seasonality, and the particular *Cebus* species inhabiting each site may also influence the pattern of seed dispersal observed and consequently the structure of plant communities.

One interesting point that arose from such site comparisons is that even though the forests are markedly different, *Cebus* responded similarly to the availability of fruits having particular traits. This is consistent with their roles as generalist frugivores and suggests that if more "specialist" or "restricted" frugivores such as spider monkeys or howlers were lost (Peres and van Roosmalen 2002), some plants would still receive disperser services from *Cebus* (e.g. at least some seeds from a majority of fruiting species would be dispersed by *Cebus* in the absence of more specialist frugivores). As forests lose more and more of the larger-bodied primates (that are often highly frugivorous), a greater proportion of seeds may go undispersed, but at least some seeds will be dispersed by *Cebus*, which points to them as being important in the future.

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Table 1. Results from logistic analyses evaluating the differences between sites and consumption in the distribution of six fruit characteristics. Consumption evaluates whether there is a difference in the trait distribution between the available and consumed fruits. Site evaluates differences in the distribution of a given fruit trait among sites. Interaction asses if diet selection occurs in some sites but not in others.

Fruit trait	Site χ^2	Diet selection χ^2	Interaction χ^2
Fruit type	15.2_{22} ns	0.7_{11} ns	2.4_{22} ns
Fruit size	11.9_{4} *	0.7_{2} ns	3.1_{4} ns
Fruit colour	41.3_{12} ***	1.1_{6} ns	6.4_{12} ns
Seed size	10.7_{4} *	0.04_{2} ns	0.9_{4} ns
Number of seeds per fruit	13.1_{6} *	0.9_{3} ns	4.1_{6} ns
Aril	6.8_{2} *	0.02_{1} ns	0.9_{2} ns

ns = non significant, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$

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Figure 1. Shannon diversity (H') and evenness (E) indeces of tree species used by *Cebus* as fruit sources in the three study sites (IGZ: Iguazú, Argentina; BCI: Barro Colorado Island, Panamá; PV: PaloVerde, Costa Rica).

Figure 2. Percentage of fruit species manipulated, consumed, and seed species swallowed from the total number available at each of the three sites during the study period. Species manipulated refers to the species handled by the monkeys for insects or any other plant part consumption. Species consumed refers to all species eaten but which seeds were not swallowed; and species swallowed were only those which seeds were swallowed (IGZ: Iguazú, Argentina; BCI: Barro Colorado Island, Panamá; PV: PaloVerde, Costa Rica).

Figure 3. Median of the time spent by *Cebus* individuals feeding on trees, and percentage of observation time spent feeding on fruit at each study site (IGZ: Iguazú, Argentina; BCI: Barro Colorado Island, Panamá; PV: PaloVerde, Costa Rica).

Figure 4. Median of travel distance and dispersal distance at each study period and site (IGZ: Iguazú, Argentina; BCI: Barro Colorado Island, Panamá; PV: PaloVerde, Costa Rica).

Figure 5. Probability of seed dispersal away from the parent plant in three different forest types (IGZ: Iguazú, Argentina; BCI: Barro Colorado Island, Panamá; PV: PaloVerde, Costa Rica).

Figure 1

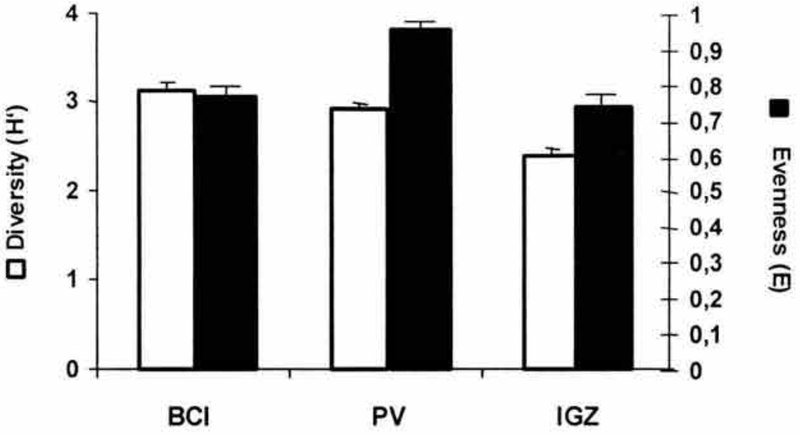

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Figure 2

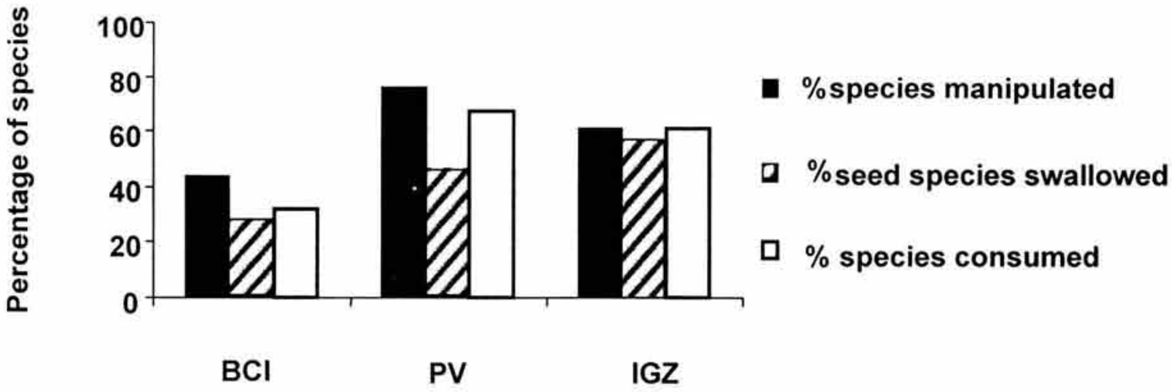

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Figure 3

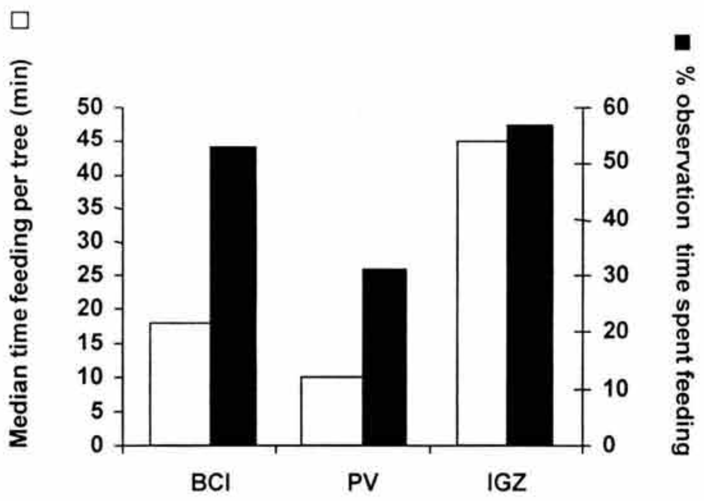

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Figure 4

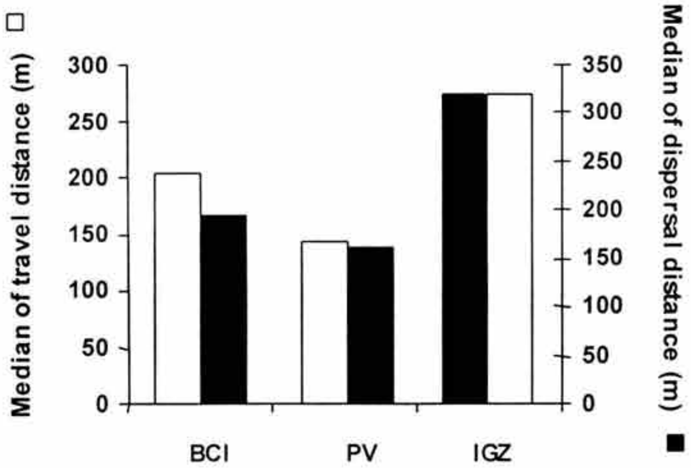

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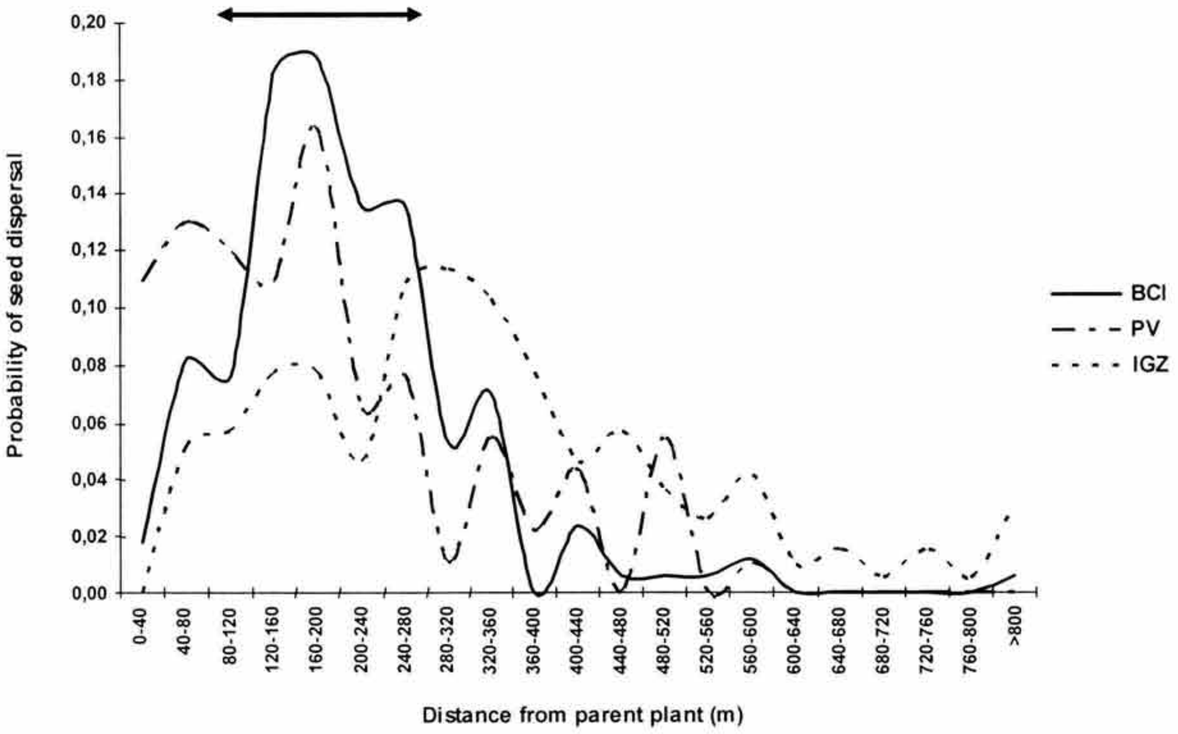
Figure 5



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CAPÍTULO II

Diversos aspectos del componente de calidad de la dispersión asociados con el patrón de defecación generado por *Cebus*

II 1. Remoción post-dispersión y germinación de semillas de especies de árboles selectas dispersadas por *Cebus capucinus* en la isla de Barro Colorado, Panamá.

(Artículo en prensa en Biotropica)

Post-dispersal removal and germination of seeds for selected tree species dispersed by *Cebus capucinus* on Barro Colorado Island, Panama.

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ABSTRACT

Dispersal quality, an important component of seed disperser effectiveness, may strongly affect the rate of plant recruitment. Here we evaluated the quality of *Cebus* monkey dispersal by comparing the secondary removal fate and germination of fresh and *Cebus* ingested seeds of nine tree species on Barro Colorado Island, Panama. Overall, rates of secondary seed removal by vertebrates were low, with most *Cebus* defecations remaining undisturbed for extended periods on the forest floor. Only four of 30 feces were completely buried by dung beetles, and we only found significantly higher vertebrate removal of defecated seeds than control seeds for one species, *Cordia bicolor*. Seed germination varied greatly between plant taxa. Seeds of 3 out of 9 species showed significantly higher percent germination after monkey-gut passage than control fresh seeds. Germination times tended to be shorter for defecated than for control seeds but were significantly different only for one of nine species - *Cecropia insignis*. Low rates of seed removal from *Cebus* feces, coupled with high germination probabilities suggest high dispersal effectiveness for *Cebus* and contrasts strongly with patterns of post-dispersal seed fate recorded for other primate species.

RESUMEN

La calidad de la dispersión, un componente importante de la efectividad de un dispersor de semillas, puede afectar marcadamente la tasa de reclutamiento de las plantas. Evaluamos la calidad de la dispersión de los monos del género *Cebus* comparando el destino de la remoción secundaria y la germinación de semillas frescas y semillas ingeridas por *Cebus* para nueve especies de árboles en la Isla de Barro Colorado, Panamá. En general, las tasas de remoción secundaria de semillas por vertebrados fueron bajas, con la mayoría de las heces de *Cebus* permaneciendo por períodos prolongados sobre el suelo del bosque. Solamente cuatro de 30 heces fueron completamente enterradas por escarabajos, y sólo encontramos una remoción por vertebrados, significativamente mayor de semillas defecadas que de semillas controles para una especie, *Cordia bicolor*. La germinación de semillas varió ampliamente entre los diferentes taxa de plantas. De nueve especies de semillas, tres mostraron un porcentaje de germinación significativamente mayor que las semillas controles luego de pasar por el tracto digestivo de los monos. Los tiempos de germinación tendieron a ser mas cortos para las semillas defecadas que para las controles, pero fueron significativamente diferentes sólo para una de nueve especies-*Cecropia insignis*. Bajas tasas de remoción de semillas de las heces de *Cebus* sumado a elevadas probabilidades de germinación sugieren una alta efectividad de la dispersión por *Cebus* y contrasta fuertemente con los patrones del destino post-dispersión de semillas para otras especies de primates.

Key words: *Barro Colorado Island,* Cebus capucinus, *dispersal effectiveness, dung beetle, germination, rodent, seasonal moist tropical forest, secondary seed dispersal, seed fate, seed removal.*

IN SPECIES-RICH PLANT COMMUNITIES EFFECTIVE DISPERSAL OF SEEDS is critical to seedling recruitment (Dirzo & Domínguez 1986, Zhang & Wang 1995, Wenny 2000, Bleher & Böhning-Gaese 2001, Schupp *et al.* 2001). The spatial pattern in which seeds are deposited and the treatment that seeds receive characterize the quality of seed dispersal by the disperser (Schupp 1993, 2002; Zhang & Wang 1995, Fragoso *et al.* 2003, Wehncke et al., in press). Important potential treatment effects of dispersers include influencing seed viability through mastication and passage through the digestive tract (Traveset & Verdú 2001), and influencing post-dispersal fate by altering the probability that seeds encounter predators and secondary dispersers (Chapman 1989, Zhang & Wang 1995, Lambert 2001, Andresen 2002, Laborde & Thompson 2004, Wehncke *et al.*, in press).

Enhanced seed germination rates have been reported for seeds following vertebrate gut passage, however effects are quite variable depending upon both the consumer and seeds consumed (Coughenour & Detling 1986, Lieberman & Lieberman 1986, Traveset & Verdú 2001). A critical dependence upon gut passage for germination is not expected given the diversity of frugivores that visit most species and the variety of ways in which seeds are handled (Lieberman & Lieberman 1986, Rowell & Mitchell 1991, Miller 1994, Overdorff & Strait 1998, Poulsen *et al.* 2002). Nonetheless, despite many reviews of the effects on seed dispersal by vertebrates (Howe & Smallwood 1982, Leighton & Leighton 1983, Gautier-Hion *et al.* 1985, Levey *et al.* 2001), we still do not know the consistency with which animals affect the germination of different plant species.

Primary dispersal by arboreal frugivores may also precede significant secondary seed removal and predation on the forest floor resulting in plant spatial distributions that are distinct from initial dispersal patterns (Chambers & MacMahon 1994, Andresen 2001, Forget *et al.* 2001, Van der Wall 2001). In neotropical forests, seeds and fruits fallen from trees or dropped by flying and arboreal consumers may be removed and consumed by terrestrial animals (Dirzo & Dominguez 1986; Forget 1993, 2001; Zhang & Wang 1995, Sánchez-Cordero & Martínez-Gallardo 1998, Andresen 1999). These include invertebrates like dung beetles and ants (Andresen 1999, 2002; Levey & Byrne 1993, Terborgh *et al.* 1993) and vertebrates like peccaries and rodents (Morris 1962, Smythe 1978, Sánchez-Cordero & Martínez-Gallardo 1998, Forget 2001, Theimer 2001, García *et al.* 2004). Postdispersal seed removal at small spatial scales by dung beetles and ants may further influence the probability of seedling establishment by preventing seed desiccation and predation (Price & Jenkins 1986, Andresen 1999, Gammans *et al.* 2004).

A variety of factors may influence whether seeds are encountered by predators and secondary dispersers on the ground. These include site conditions, such as litter coverage, influencing visual cues, (Schupp 1988a, b; Willson 1988), seed density and proximity to fruiting trees influencing foraging patterns (Janzen 1970, 1971; Schupp 1988b, Forget & Milleron 1991, Forget 1993, Fragoso *et al.* 2003), and the presence of fecal material generating olfactory cues (Zhang & Wang 1995, Lambert 2001, Wehncke *et al.*, in press). Thus, we might expect contrasting seed fates depending on both where seeds are deposited, and how seeds are handled and consumed.

Here we examine the critical effects of seed consumption on the dispersal effectiveness of the white-faced monkey, *Cebus capucinus* (Linnaeus 1758). Previous studies of this primate indicate its potential as an exceptionally effective seed disperser carrying seeds long distances, and depositing seeds in small clumps with relatively little fecal material (Wehncke *et al.*, 2003). Here we evaluate:

1. The effect of the presence of *Cebus* feces on seed removal by invertebrates and vertebrates.
2. The effect of seed deposition microsite (beneath and 20 m away from fruiting trees), on the intensity of seed removal by invertebrates and vertebrates, and
3. The percentage and rate of seed germination for a sample of species defecated by *Cebus*.

METHODS

STUDY SITE. -- The study was conducted in seasonally moist tropical forest on Barro Colorado Island (BCI), Panama (9°09'N, 79°51'W), (Croat 1978, Foster & Brokaw 1982). The climate on BCI is seasonal with a dry period from late December through mid-April and a wet season having peak rainfall in October-November. Rainfall averages 2600 mm year^{-1} and annual temperature averages 27°C. A description of the flora, fauna and ecology can be found in Croat (1978), and Leigh (1999). The most abundant vertebrate seed predators and secondary dispersers on BCI are agoutis (*Dasyprocta punctata*, Gray 1842); red-tailed squirrels (*Sciurus granatensis*, Humboldt 1811); the spiny rat (*Proechimys semispinosus*), (Tomes 1860); pacas (*Coniculus paca*), (Linnaeus 1776) and peccaries (*Tayassu tajacu*), (Linnaeus 1758). The study was carried out early in the wet season (June 1999) when fruit availability is highest on BCI (Foster & Brokaw 1982).

CEBUS EFFECTS ON VERTEBRATE SEED REMOVAL. -- To examine how *Cebus* monkeys influence post-dispersal seed removal rates we placed seeds with and without fecal material at two potential seed deposition sites: below and 20 m away from the crowns of fruiting *Cordia bicolor* A. DC., (Boraginaceae) trees. At each site we evaluated the fate of seeds of five species either imbedded in *Cebus* feces, or collected directly from fruits and set out without feces (controls). Control and fecal-embedded seeds were placed in plastic bowls 15 cm diameter, 4 cm tall buried flush with the soil surface. The number and species of seeds used for this experiment were selected, as they were representative of seeds found in the feces of *Cebus* during the study period (Wehncke *et al.* 2003). Treatment and control bowls were placed 1 m apart and each contained three seeds of *C. bicolor*, two seeds of *Licania hypoleuca* Benth. (Chrysobalanaceae), one seed of *Lacmellea panamensis* (Woodson) Markgr. (Apocynaceae), one seed of *Rheedia edulis* (Seem.) Planch & Triana (Guttiferae), and five seeds of *Hasseltia floribunda* Kunth (Flacourtiaceae). In total, paired treatment and control bowls were placed at ten below-crown sites and at ten paired sites 20 m away.

C. bicolor was selected as the focal species in this study because its fruits are among the most frequently consumed by *Cebus* (see Appendix in Wehncke *et al.* 2003), and because fruiting trees are abundant, widely distributed in the study area and had large fruit crops during the study period. As we were unable to distinguish seed predation from secondary dispersal, we refer here to seed removal. In addition, we did not distinguish between seed removal by small and large rodents, and by other vertebrates. The steep sides of the plastic bowls used in this experiment prevented seeds from being removed by dung beetles. Transparent plastic shelters constructed 50 cm above the soil surface also protected seeds from litter coverage and from rain from washing away fecal material. The number of seeds removed from each bowl was recorded after 2, 5, 13, and 27 days of first placement. After the last census no more removal events were recorded. We used the Fisher Exact Test to test if the presence of feces and deposition site had any effect on seed removal.

CEBUS EFFECTS ON INVERTEBRATE SEED REMOVAL. -- We performed a second experiment to test whether *Cebus* gut passage and the proximity to fruiting trees had any effect on the rate of seed removal by dung beetles and ants. Seeds of three species were placed directly on the soil surface at sites directly beneath fruiting *C. bicolor* trees and 20 m from fruiting trees as before. Seeds used in this experiment were from *Miconia argentea* (Sw.) DC. Melastomataceae (0.5 mm length), *Cecropia insignis* Liebm. Cecropiaceae (1.25 mm length) and *C. bicolor,* (8 mm length). Individual species were placed at separate locations > 1m apart and were either enclosed in *Cebus* feces or were removed directly from ripe, undispersed fruits. In total, one pair of fecal enclosed and fresh seed treatments for each species was placed below a different *Cordia* tree and non-*Cordia* site each day for five days.

To mimic the observed composition of *Cebus* defecations, each simulated fecal sample (average weight = 7.6 ± 3 g) contained 2,500 *M. argentea* seeds, 1,000 *C. insignis* seeds or 1 *C. bicolor* seed. These numbers were obtained by dissecting fecal samples produced by *Cebus* monkeys and represent the modal number of seeds of these species in total fecal samples. Fresh seeds collected from ripe fruit were placed out in numbers characteristic of the mean clump size produced by passive dispersal of these species beneath the crowns of fruiting trees and consisted of 100 *M. argentea* seeds, 50 *C. insignis* seeds and 3 *C. bicolor* seeds. Sets of seeds were observed for 6 hours after the time they were set out. We registered the time of complete removal of feces and seeds, and also the time of arrival of each different beetle and ant species. Beetles were classified into two types according to the way feces were processed: "tunnelers" immediately buried seeds and feces at the site they were encountered whereas "rollers" removed seeds up to distances ranging between 6-250 cm, (50.8 ± 55.1 cm, $N = 18$) before burial. Beetles were preserved in 70% alcohol for later identification. At the end of the experiment, we determined how many seeds were left and the proportion of fecal material removed and buried. The mean number of *C. insignis* and *M. argentea* seeds removed from the two habitat types were compared using the Paired Samples "t" Test.

SEED GERMINATION. -- To examine whether seeds survive passage through the gut of *Cebus*, we removed seeds from fresh (<2 d old) *Cebus* feces and from fruits of the same species dropped to the ground during primate feeding bouts. Germination tests were performed on nine species (Table 1) representative of the wide range in size and morphology of seeds consumed by *Cebus* (see Appendix in Wehncke *et al.* 2003). Small seeds (< 0.5 cm) of 6 different species (*C. insignis*, *Cecropia obtusifolia* Bertol., *Ficus yoponensis* Desv., *H. floribunda, Miconia affinis* DC., and *M. argentea*) were placed on filter paper on Petri-dishes, and were kept in a growth chamber (12 h at 60 μmol $m^{-2} s^{-1}$, red: far red 1.65, at 30°C; 12 h dark at 25°C). Large seeds (> 0.5 cm) of *C. bicolor, Cordia lasiocalyx* Pittier, and *R. edulis*) were placed in trays containing a mixture of sterilized soil and sand in a 3:1 proportion, and placed in a screened growing house (*c.* 20% full sun). Seeds were not washed before sowing in order to simulate natural conditions for germination. Seeds were watered when needed and emergent seedlings were counted and removed every 2-5 days. The number of seeds that germinated at the end of the experiment from fecal samples vs. dropped fruits was compared using the Mantel-Haenszel Test, and the percentage and rate of seed germination were calculated. Germination trials ended three weeks after no further germination. Median germination times were compared using the Mann-Whitney Test.

RESULTS

VERTEBRATE SEED REMOVAL. -- After 27 days of observations, four of five species considered in this experiment experienced low levels of seed removal ranging from 8% for *C. bicolor* to 38% for *L. panamensis*. At the end of the study the numbers of seeds removed did not differ significantly between sites below and away from *Cordia* trees although more seeds tended to be removed from the below tree sites for three of the four species studied (Table 2). Presence of fecal material had a significant positive effect on removal only for *C. bicolor* seeds, with a marginal effect for *L. hypoleuca* (Table 2). Seeds of *H. floribunda* were excluded from this analysis, because ants were observed entering the bowls and consuming the seeds. Furthermore, five seeds of *C. bicolor* and 29 seeds of *H. floribunda* germinated in situ during 27-d period. Only 5 days were needed for 23 *H. floribunda* seeds to germinate.

SEED REMOVAL BY DUNG BEETLES AND ANTS. -- Most (24/30) feces were visited by dung beetles or ants over the 5 days of the study. Two beetle species also visited seeds without fecal material but did not remove them. Dung beetles arrived at the feces on average after 65 ± 53 min ($N = 24$). Only four feces were buried completely, and therefore most of fecal enclosed seeds remained on the forest floor for an extended period. A total of 53 beetle species and 9 ants, 2 species, were observed at seed stations (Appendix). An average of 1.8 ± 1.3 (range 0-4) different beetles arrived at each fecal sample during the study ($N = 30$). During the first hours after the placement of feces on the floor, rollers were commonly attracted first. The mean number of beetles attracted to each fecal sample was the same in the two microsites (mean number of beetles for the two microsites = 1.7 ± 1.3, $N = 15$).

Beetles arrived at similar times to feces placed below and away from fruiting trees (mean time of beetle arrival: 68 ± 58 min, $N = 11$ and 62 ± 52 min, $N = 13$; respectively). All 11 of 30 feces rolled into balls by beetles contained seeds of *M. argentea* and *C. insignis*. In contrast, only two out of 30 *C. bicolor* seeds imbedded in feces were rolled away by dung beetles. Beetles moved dung balls at an average distance of 51 ± 55 cm ($N = 18$, range: 6-250 cm). Significantly more seeds of *M. argentea* (mean number of seed removed: 1220 ± 770, $N = 15$) and of *C. insignis* (mean number of seed removed: 490 ± 310, $N = 15$) imbedded in feces were removed by dung beetles from sites away from *C. bicolor* trees ($P < 0.05$ for both), than from sites below *C. bicolor* trees (mean number of seed removed: 917 ± 885, $N = 15$) and of *C. insignis* (mean number of seed removed: 367 ± 354, $N = 15$). Two ant species removed 30/500 seeds of *M. argentea* and 30/250 seeds of *C. insignis* lacking fecal material and from outside *Cordia bicolor* trees. We did not test differences in ant removal between locations because these data represent only two cases of seed removal by ants. Ants did not remove seeds from fecal material.

SEED GERMINATION. -- *Cebus* ingestion altered seed germination success relative to uningested seeds for almost all species tested. Effects of *Cebus* ingestion however, were not consistent among species. Of the nine species studied four species had significantly higher germination of defecated than uningested seeds, and two species had significantly lower germination (Table 3). For the three remaining species there were either no significant differences in germination success or overall germination rates were too low to assess treatment effects. Gut passage had very little effect on the rate of seed germination. Seeds of *C. insignis* ingested by *Cebus* germinated significantly faster than control seeds (U = 174, df = 1, P = 0.008), but median time to germination was only a day earlier for defecated seeds. Median germination times for the remaining species varied from 6 days (*Hasseltia*) to 77 days (*Rheedia*) and were not significantly different between treatments.

DISCUSSION

Two factors that may alter patterns of primary seed dispersal in Neotropical forests are the presence of fecal material around seeds (Janzen 1982a, b; Chapman 1989, Howe 1989, Zhang & Wang 1995) and the presence of high densities of fruits and seeds at sites where seeds are deposited (Janzen 1970, 1971; Sánchez-Cordero & Martínez-Gallardo 1998). Here, we show that for seeds dispersed by *Cebus capucinus*, neither the presence of feces, nor the seed deposition microsite had significant effects on post-dispersal seed removal by invertebrates and vertebrates. Furthermore, ingestion of seeds by *Cebus* failed to show strong and consistent effects on the success or rate of seed germination among the species evaluated.

These results are in contrast to previous studies showing that mammalian dung can attract dung beetles (Estrada & Coates-Estrada 1986, 1991; Estrada *et al.* 1993, Andresen 2001) and rodents (Janzen 1986, Andresen 1999). At least in the Neotropics, some evidence suggests that it is the pattern in which seeds are defecated that is the crucial factor determining the rates of seed removal (Zhang & Wang 1995, Wehncke *et al.*, in press). Seeds are deposited by *Cebus* in a scattered manner along with relatively small amounts of fecal material resulting in low seed removal rates (Zhang & Wang 1995, Wehncke *et al.*, in press). We predicted that because a clumped pattern of defecation characteristic of most primate species constitutes a major visual or olfactory stimulus for seed predators, seed survival in scattered, small fecal clumps should be higher. In this study we found strikingly low seed removal rates from *Cebus* defecations, either by dung beetles, ants, or rodents. Other important dispersers of species consumed by *Cebus* on BCI (bats, tapirs, howler and spider monkeys) are also capable of equally long-distance seed movement, however they commonly deposit seeds in large clumps at feeding roosts, latrines and/or sleep trees (Julliot 1986, Zhang & Wang 1995, Fragoso 1997, Thies 1998, Schupp *et al.* 2002, Fragoso *et al.* 2003, Wehncke *et al.* 2003). However, we should mention that Julliot (1997) working with howler monkeys and Rogers *et al* (1998) with gorillas showed that seeds deposited in clumped patterns may also experience increased seedling survival.

On BCI, studies have generally reported high levels of secondary seed dispersal and predation by rodents (Forget & Milleron 1991; Forget 1992, 1993, 1996; Forget *et al.* 2001), however, it may be highly variable depending on season and site. Seasonal variability in food availability coupled with spatial variation in food abundance are most likely to strongly affect the fate of rodent removed seeds (Vander Wall 1990, Forget *et al.*

2001). For example, on BCI, agoutis, *D. punctata,* hoard considerably more seeds than they eat during the period of high fruit abundance (May-August) when this study was conducted (Smythe 1978, Forget *et al.* 2001). Thus, rodent population density and food availability may interact to create areas of low or high secondary seed dispersal or predation (Notman *et al.* 1996; Forget *et al.* 2000, 2001). Low removal rates reported here may not necessarily translate to significantly higher recruitment rates for *Cebus* dispersed seeds. Here, we referred only to short-term seed survival after deposition, whereas the best site for seed survival may not necessarily be the best site for sapling recruitment. Further studies on seed fate are needed to confirm this.

Although some studies report density-dependent seed removal for several plant species in the Neotropics (Howe *et al.* 1985, Schupp 1988a, Sánchez-Cordero & Martínez-Gallardo 1998), our results agree with those that reported an absence of distance effects (Molofsky & Fisher 1993, Terborgh *et al.* 1993) or levels of predation independent of habitat (Forget & Milleron 1991). Lambert (1997, 2001) in the Paleotropics found similar independence of predation with microhabitat and treatment but, by contrast, showed severe levels of post-dispersal seed predation. Because our study focused on a selected set of seed species swallowed and dispersed by *Cebus*, and a single tree species was used to evaluate microsite effects, we should be careful for the moment of making general conclusions. However, these species were selected because they well represented species dispersed by *Cebus* at the study period and those species able to be removed by potential predators of small to medium-sized seeds (up to *c.* 1.5 cm long). In summary, low rates of seed removal in fruit and seed-rich areas may depend on food availability elsewhere in the forest and on the quality of food resources available (Brewer 2001, Forget *et al.* 2001). Therefore, we could suggest that high availability and/or better quality of food resources in other parts of the forest might explain overall low rates of seed removal in this experiment during the study period.

In this study, similar mean numbers of dung beetles were attracted to locations below fruiting *C. bicolor* trees and to locations with no fruiting trees. The time of first arrival of dung beetles was also similar in both sites. Seed burial by dung beetles is considered to have a strong influence on seed survival by preventing seed predation and desiccation (Andresen 1999, 2002). However, the depth at which beetles bury seeds can also reduce germination success (Dalling *et al.* 1994, Shepherd & Chapman 1998, Feer 1999). In this study most of the seeds remained imbedded in feces on the forest floor and experienced low removal rates. In the case of the largest seeded species, *C. bicolor*, only 2/30 seeds were buried by dung beetles. As a consequence, species most likely to benefit from escape from rodent predation through burial, and most likely to successfully emerge from beneath several centimeters of soil may be least likely to be incorporated into beetle dung balls.

Earlier work has indicated that *C. capucinus* is a very effective (e.g. *sensu* Schupp 1993, 2002) seed dispersal agent (Zhang & Wang 1995, Wehncke *et al.* 2003). On BCI it has been shown that *Cebus* manipulate and consume a remarkably high diversity of fruit species, from which seeds of the majority are found intact in feces in a viable state (Wehncke *et al.* 2003). Combinations of characteristics such as short feeding bouts, asynchronous small defecations of individuals within the group, and short gut retention times contribute to the seed defecation pattern produced by *Cebus*. As a consequence of these characteristics most of the seeds receive a gentle treatment by *Cebus,* they are dispersed to long distances, and are deposited in a widely spaced spatial pattern. These are among the clearest advantages accruing to those ingested seeds, because they have the opportunity to escape from the increased risk of mortality around the neighborhood of the parent plant, and to colonise new and potentially more favorable microsites for seedling establishment (Howe & Smallwood 1982).

According to Howe's (1989) 'scatter- and clump-dispersal' hypothesis, 'scatter-dispersed' plant species are unlikely to evolve tolerance against density-dependent factors (chemical and/or mechanical defenses against competitors, seed predators and pathogens) because they recruit to the seedling stage as isolated individuals. Here we found a high variation of the effect of *Cebus* ingestion on germination success among seed species, and almost no effect on the rate of germination. We suggest that although seed deposition patterns have important implications for short-term seed survival (Wehncke *et al.*, in press) at least in a neotropical dry forest, variations in seed ingestion and handling between and within dispersers and habitats may contribute to attenuate any possible adaptation of plants to differences between scatter- and clump-dispersal strategies.

Finally, as the dispersal quality provided by any given animal is not constant (Wehncke *et al.*, in press) and may depend on the particular ecological scenario where dispersal takes place, the relationship among a series of factors (environmental and those occurring between animal frugivory, seed deposition and seed fate) influence the ultimate fate of the seed dispersed. Although here we provide data regarding the possible role of post-dispersal agents and effect of gut passage on seed germination, more comparative work is still needed to evaluate the relative contributions of members of diverse disperser communities to plant recruitment success in contrasting habitats.

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Table 1: Total number of species of seeds defecated (treatment) and fresh (control) used in germination experiments. Total number of seeds and days of observation. Number of replicates are in brackets. The first 6 species were germinated in a growth chamber.

Species of seeds	Number of defecated seeds (trials)	Number of control seeds (trials)	Total seeds studied	Total days
C. insignis	350 (15)	350 (15)	700	59
C. obtusifolia	40 (2)	60 (2)	100	43
F. yoponensis	64 (3)	64 (3)	128	43
H. floribunda	27 (4)	90 (6)	117	47
M. affinis	100 (2)	100 (2)	200	29
M. argentea	1013 (22)	1016 (22)	2029	64
C. bicolor	95 (22)	28 (10)	123	12
C. lasiocalyx	53 (11)	53 (11)	106	24
R. edulis	14 (4)	10 (3)	24	12

Table 2. Seed removal by vertebrates according to type of microhabitat and presence or absence of *Cebus* fecal material (see methods).

Species of seeds	Seed removal from two types of microhabitats. Percentage of seeds removed Below (N)	Outside (N)	Fisher Exact Test (P)	Seed removal from feces and controls Percentage of seeds removed Feces (N)	No feces (N)	Fisher Exact Test (P)
C. bicolor	12% (60)	3% (60)	0.163	13% (60)	2% (60)	0.032
L. hypoleuca	15% (40)	10% (40)	0.737	20% (40)	5% (40)	0.087
L. panamensis	33% (8)	40% (8)	1.00	62% (8)	12% (8)	0.119
R. edulis	17% (5)	0% (5)	1.00	20% (5)	0% (5)	1.00

Table 3: Percentage of germination for defecated vs. control species of seeds. Numbers of replicates detailed in Table 1. (*): cases in which germination percentages were higher for defecated than for control seeds.

Seed species	Defecated seeds (N)	Control seeds (N)	Mantel-Haenszel Chi-square	P
C. insignis	83% (350)	100% (350)	43.199	< 0.01
C. obtusifolia	67% (40)	10% (60)	42.948	< 0.01*
F. yoponensis	85% (64)	0 (64)	---	---
H. floribunda	84% (27)	77% (90)	4.950	< 0.05 *
M. affinis	96% (100)	82% (100)	8.995	< 0.01 *
M. argentea	64% (1013)	99% (1016)	457.694	< 0.01
C. bicolor	18% (95)	0 (28)	---	---
C. lasiocalyx	20% (53)	41% (53)	0.816	> 0.05
R. edulis	68% (14)	71% (10)	2.438	> 0.05

Table 4: Mean time at which the 50% of defecated and control seeds germinated.

Species	Defecated seeds		Control seeds	
	Mean T50 (days)	Rank Sum	Mean T50 (days)	Rank Sum
C. insignis	7	171	8.5	294
C. obtusifolia	10.5	4	14	6
F. yoponensis	11	9	12	12
H. floribunda	6.5	16	5.5	39
M. affinis	11	4	14	6
M. argentea	15.3	451.5	16.3	538.5
C. bicolor	35.5	343	38	185
C. lasiocalyx	31.5	134	30	119
R. edulis	70.5	14.5	77	13.5

Appendix. Species of dung beetles attracted to *Cebus capucinus* feces. Number of individuals captured during the experiment in each ecological category: tunnelers = 32, rollers = 26.

Hybosoridae

Anaides fossulatus Westwood 1846, Venezuela

Coilodes castaneus Westwood 1846, Colombia, Costa Rica, Nicaragua

Scarabaeidae Scarabaeinae

Ateuchus candezei (Harold)	Tunneler
Ateuchus howdeni Kohlmann	Tunneler
Cathidium ardens Bates	Tunneler
Canthidium elegantulum Balthasar	Tunneler
Canthidium haroldi Preudhomme	Tunneler
Canthidium tuberifrons Howden & Young	Tunneler
Canthon aequinoctialis Harold	Roller
Canthon angustatus Harold	Roller
Canthon cyanellus sallei Harold	Roller
Canthon euryscelis Bates	Roller
Canthon moniliatus Bates	Roller
Canthon septemmaculatus (Latreille)	Roller
Canthon subhyalinus Harold	Roller
Onthophagus dicranius Bates	Tunneler
Onthophagus sharpi Harold	Tunneler

II 2. Dispersión de semillas y patrones de defecación por *Cebus capucinus* y *Alouatta palliata*: consecuencias en la eficiencia de la dispersión de semillas.

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Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: consequences for seed dispersal effectiveness

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Abstract: Primates are primary seed dispersers for many tropical tree species. Different species of primates vary considerably in ranging and feeding behaviour, seed processing, and in seed defecation patterns. Here we compare the role of two arboreal primate species, howlers (*Alouatta palliata*), and white-faced monkeys (*Cebus capucinus*) as seed dispersers in a tropical dry forest in Costa Rica. We found that *Cebus* produce smaller defecations, spend shorter times feeding per tree, have longer seed dispersal distances, and produce a more scattered pattern of seed deposition in the forest than *Alouatta*. In addition, *Cebus* moved more frequently between trees, and consumed fruits of more species than *Alouatta*. We examined the consequences of the contrasting defecation patterns produced by *Cebus* and *Alouatta* on the early seed fate of *Acacia collinsii*. We found that quantity, but not the identity (*Cebus* vs. *Alouatta*) of faecal material affected post-dispersal activity. Seeds in scattered faeces, sufficiently apart from each other (the common defecation pattern of white-faced monkeys), had higher short-term survival than seeds in clumped patterns of faeces (the pattern associated with *Alouatta*).

Key Words: *Acacia collinsii, Alouatta palliata, Cebus capucinus*, Costa Rica, defecation patterns, dispersal effectiveness, post-dispersal, primates, seed dispersal, seed removal, tropical dry forest

INTRODUCTION

Seed dispersal has a direct effect on the distribution of individuals within populations and on the colonization of new habitats, which in turn affects the rates of gene flow and the genetic structure of plant populations (Dirzo & Domínguez 1986, Hamrick *et al.* 1993, Martínez-Ramos & Soto-Castro 1993, Schupp 1988). Seed dispersal is also involved in the dynamics of forest regeneration and therefore in the long-term maintenance of plant communities (Lambert & Garber 1998, Webb & Peart 2001). Given the relevance of the dispersal process many people have tried to disentangle the complex phenomena occurring between the production of a seed and the establishment of a new plant (Jordano & Schupp 2000). In many instances frugivorous animals mediate this process, and consequently the ultimate fate of seeds depends on the effectiveness of the frugivores consuming them.

The effectiveness of a frugivorous species as a seed disperser has been defined as the contribution it makes to plant fitness (Fleming *et al.* 1993, Schupp 1993). Effectiveness in turn depends on the quantity of seeds dispersed and on the quality of dispersal provided to each seed (Herrera *et al.* 1994, Jordano & Schupp 2000, Schupp 1993). As pointed out by Chapman (1989) and Schupp (1993), while much emphasis has been given to the quantity component, the quality component of seed dispersal (such as the location and pattern of seed deposition) may be the single most important factor determining the final fate of a seed (Janzen 1982a, 1986; Schupp 1993, Zhang & Wang 1995).

The quality component of dispersal includes fruit handling, seed treatment, dispersal distance and the type of site where the seed is deposited. Once a seed is deposited, the probabilities of germination and establishment depend on the physical environment and on the likelihood of encountering post-dispersal seed predators and secondary dispersers. Characteristics of the

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faecal material surrounding dispersed seeds may strongly influence these probabilities. Faecal matter modifies the local environment of seeds, altering moisture and nutrient supply (Coughenour & Detling 1986), and can be used as a visual or olfactory cue by seed predators (Andresen 1999, Chapman 1989, Howe 1989, Janzen 1982a, b; Rowell & Mitchell 1991, Zhang & Wang 1995). It is therefore possible that differences in dispersal effectiveness among frugivorous species are related, at least partially, to differences in their patterns of defecation (Andresen 1999, Zhang & Wang 1995).

In neotropical forests, Chapman (1989) and Julliot (1996a) reported the important role played by *Ateles geoffroyi* (Kuhl 1820), *Alouatta palliata* (Gray 1849), and *Cebus capucinus* (Linnaeus 1758) as seed dispersers. *Cebus* and *Alouatta* constitute between 25 and 40% of the frugivore biomass in the tropical forests they inhabit (Chapman 1995, Eisenberg & Thorington 1973) and consume and disperse large quantities of fruits and seeds (Chapman 1995, Estrada & Coates-Estrada 1984, Rowell & Mitchell 1991). Different species of primates may differ in their dispersal effectiveness depending on their behaviour, physiology, morphology and defecation patterns (Howe 1989, Janzen 1983b, Levey 1987, Lieberman & Lieberman 1986, Poulsen *et al.* 2002, Zhang & Wang 1995).

In this study we characterized the seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata* (hereafter *Cebus* and *Alouatta*, respectively), and experimentally evaluated the consequences of the faecal material on the short-term survival of *Acacia collinsii* Saff. seeds, a common small tree (up to 5 m) at our study site. Both species of primate inhabit the same area in a tropical dry forest of Costa Rica and differ greatly in terms of behaviour, physiology and morphology. We first made a general characterization of *Cebus* and *Alouatta* as seed dispersers. Because the quality component of dispersal could fluctuate if animals exploit resources that are unevenly distributed in time and space (like most fruiting trees), we explored how some attributes like diet, and seed dispersal distances vary in space and time. Our previous observations indicate that *Cebus* monkeys tend to defecate individually in space and time creating a scatter of small defecations. In contrast, troops of *Alouatta* defecate simultaneously at the same place producing large areas of clumped defecations. We evaluated this spatial pattern of droppings generated by the two species. Based on our preliminary data and on studies revealing an important effect of faecal quantity on seed survival (Andresen 2002, Janzen 1982a, 1986; Zhang & Wang 1995), we hypothesized that because high quantity of faecal material constitutes a major stimulus (visual or olfactory) for seed predators, seed survival in *Cebus* faeces should be higher than in *Alouatta* faeces. This hypothesis was evaluated by means of a field experiment simulating the natural droppings of *Cebus* and *Alouatta*.

METHODS

Study site

This study was conducted in the Palo Verde National Park, Costa Rica (10° 21′ N, 85° 21′ W). The site is described by Tosi (1969) and Vaughan *et al.* (1982). Palo Verde is about 20 000 ha and includes several ecosystems such as tropical dry deciduous forest, evergreen forest, seasonal swamp and marshes. The climate is characterized by a marked dry season from mid-December to the end of May. Mean annual rainfall is 1500–2000 mm.

Study species

The black howler monkey, *Alouatta palliata*, is one of the largest primates in Central and South America, with a body mass ranging from 7–9 kg. Troop sizes lie in the range 3–26 individuals and overall mean densities estimated in Palo Verde were 69 individuals km^{-2} (Massey 1987). Diet consists mainly of leaves but it also eats fruits (Estrada & Coates-Estrada 1984, 1986; Glander 1975, Massey 1987, Milton *et al.* 1980).

Cebus capucinus ranges from Honduras to Ecuador (Wolfheim 1983) and is a relatively small primate with a body mass ranging from 2–3.5 kg (Milton 1984). It consumes fruit, but also vertebrates, shoots, eggs and invertebrates (Milton 1984, Mitchell 1989, Moscow & Vaughan 1987, Oppenheimer 1968). Troop sizes at Palo Verde vary between 15 and 23 individuals (Massey 1987, Moscow & Vaughan 1987), with overall mean densities of 15 individuals km^{-2} (Massey 1987).

Feeding, movements, and distribution of faeces

To describe the foraging behaviour and dispersal characteristics of the two primate species, two groups of *Alouatta* (group L: 8 individuals; group J: 10 individuals), and two of *Cebus* (group P: 16 individuals; group R: 22 individuals) were followed for a total of 47 d throughout the study (dry season: April–July 2000, *Cebus*: 14 d, *Alouatta*: 10 d; wet season: July–September 1999, *Cebus*: 11 d, *Alouatta*: 12 d). Our observations began at sunrise (06h30) when monkeys were leaving their sleeping sites, or at any time after finding the group, and finished at sunset (18h00) when they stopped in trees to sleep. Seeds handled by monkeys were categorized as spat out, damaged, and swallowed. Whenever possible, every tree used as a fruit source was identified to the species level.

Different attributes of the seed dispersal provided by *Cebus* and *Alouatta* such as the time spent eating in fruiting trees, and the dispersal distances were evaluated. We used the Mann–Whitney U-test to evaluate the differences in time spent eating in fruiting trees between monkey species. We used an Analysis of Variance to test the effect of species of monkey, season and the interaction on the number of species h^{-1} and fruiting trees h^{-1} visited. Faecal samples were collected from the forest floor or from understorey vegetation while following the monkeys. These samples were taken to the laboratory and all seeds were separated from faeces, counted, measured, and identified to species. Seeds < 1 mm long were not counted, and their numbers in faeces were estimated within categories (few: 20–50, many: 50–100, numerous: > 100 seeds). When available from faeces, a sample of 10–40 seeds was used to test viability. We distinguished, mapped, and counted all droppings reaching the forest floor. We calculated the distances between nearest-neighbour droppings. Thus, by grouping number of droppings within each class of distance, we obtained a simple measure of dispersion for both species of monkey. We tested differences in the frequency of faeces deposited at different distances between the two monkey species using the χ^2 test. Seed dispersal distances depend on the average time of passage through the digestive tract and on the distance travelled since the seeds were consumed. The daily distances travelled by the troops, the position of all trees used as food sources, and all the locations where defecations were deposited were estimated by using a GPS (Garmin 12), compass and pedometer. We used these measurements, along with estimations of the average time of passage of seeds throughout the guts of monkeys, to estimate mean seed dispersal distances. The straight-line distances between trees and the position of the group after seed retention time were calculated directly on maps. Mean seed retention times through *Cebus* (1.40 h, range 0.75–3 h) and *Alouatta* (18 h, range 16–25 h) digestive tracts were obtained from studies with captive monkeys (*C. capucinus*, Wehncke *et al.* 2003; and *A. palliata*, Estrada & Coates-Estrada 1984, Julliot 1996a, b; Milton *et al.* 1980).

Effect of defecation patterns and faecal identity on seed removal

To assess whether the quantity of faecal material and the identity of faeces influence post-dispersal seed removal, we performed a field experiment during the dry season of 2000. We simulated the contrasting patterns of defecation by using a factorial design with quantity (three levels: 0, 5 and 50 g of faeces) and identity (two levels: *Alouatta* and *Cebus*) of faecal material as factors, and evaluated the effects of these treatments on the seed removal of *Acacia collinsii*. *Acacia collinsii* fruits are legumes with an edible sweet pulp. On the one hand, this experiment required that a high number of seeds could be available and on the other, we are interested in the consequences of the faecal material on post-dispersal seed removal. We used this species because of its high availability of seeds and because they are actively sought by rodents (Wehncke and Numa, pers. obs.). Each treatment consisted of 10 *A. collinsii* seeds (average size: 0.54 ± 0.08 cm, n = 20) embedded in the surface of the assigned amount and type of faecal material. Controls consisted of 10 seeds without faecal material. We used 10 seeds because this approximates to the maximum number of seeds of this species found in a single dropping of *Cebus* and to the average number of seeds in these ranges of size found in a single dropping of *Alouatta*. Only fresh faecal samples (no older than 1 d) and mature seeds were used in the experimental treatments. Faecal samples were collected from the field and kept at 4 °C, and all the original seeds were removed before the experiment. Twenty replicates of each treatment were randomly distributed along a transect in the forest. Treatments were placed at least 25 m apart from each other. To have a qualitative estimate of the proportion of sites with rodent visitation, we recorded rodent activity by daily censuses of footprints on sand beds that were set around our experimental sites. Because our main interest was to evaluate the effect of faecal material as a visual or olfactory cue to seed predators, and given that faeces were completely dry after the third day, our censuses were restricted to a 5-d period. We assumed that it is during this period when the influence of faeces is maximum. The effect of the amount and identity of faecal material on seed removal was evaluated by means of a proportional hazard survival model (Fox 1990, Muenchow 1986). This procedure is a semi-parametric regression model that analyses the effect of explanatory variables on survival times (SAS Institute 1995), and produces a Likelihood-Ratio test that approximates to a Chi-square test (Fox 1993). Statistical analyses were performed using the computer software JMP 3.1. (SAS Institute 1995).

RESULTS

Feeding, movements and distribution of faeces

Cebus and *Alouatta* differed in seed handling (Appendix I). During the study period, *Cebus* and *Alouatta* consumed a total of 33 and 10 species of fruits, respectively (Appendix II). *Cebus* defecated a greater percentage of faecal samples containing seeds (*Cebus*: 98%, n = 162; *Alouatta*: 54%, n = 68). While *Cebus* swallowed seeds of up to 1.5 cm long (although those > 0.9 cm were commonly spat out), *Alouatta* swallowed seeds of up to 2.4 cm. Most of the seeds in the faeces of both species were found intact. From approximately 4200 seeds from different species found in *Cebus* faeces, only 20 seeds of two species were found destroyed. We found no damaged seeds in *Alouatta* faeces. *Cebus* spent less time feeding per fruiting tree than *Alouatta* (median = 10 min, n = 119 for *Cebus*; median = 20 min, n = 23 for *Alouatta*, Mann–Whitney U = 14, P = 0.0002). Of the three factors evaluated only the species of monkey yielded significant results. *Cebus* visited more fruiting trees (median = 1 tree h^{-1}, n = 22 for *Cebus*; median = 0.3 trees h^{-1}, n = 8 for *Alouatta*, Mann–Whitney U = – 2.2, P = 0.03) and species h^{-1} than *Alouatta* (median = 0.8 species h^{-1}, n = 22 for *Cebus*; median = 0.2 species h^{-1}, n = 8 for *Alouatta*, Mann–Whitney U = – 2.5, P = 0.01).

In general, the distances travelled by monkeys in 1 d tended to be approximately straight lines. Mean seed dispersal distances produced by *Cebus* were significantly different between seasons (154 ± 121 m, n = 48 and 210 ± 160 m, n = 45, for wet and dry seasons, respectively, Median test = 27, P < 0.05). *Cebus* are very mobile animals; the highest probability (0.45) of movement away from trees was recorded in the first 10 min, less than the mean seed transit time through their gut (100 min, Wehncke *et al.* 2003), in other words, before defecation. We do not have this kind of data for *Alouatta* because during this study fruit-eating events were very scarce.

There were only 8 out of 81 observations in which more than one individual of *Cebus* defecated simultaneously in space. In contrast, almost all individuals of a group of *Alouatta* defecated simultaneously in space before moving to the next feeding tree (33 observations), thus creating areas of defecation. When a dropping of *Alouatta* dung reached the floor, most neighbouring faeces were deposited within 1–5 m (67% of their faeces), creating areas of high concentration of faeces and seeds (Figure 1a). In contrast, *Cebus* deposited 50% of their faeces at distances > 10 m from each other (Figure 1b). *Cebus* and *Alouatta* differ significantly in the distribution of faeces deposited at different distances ($\chi^2 = 12.4$, $P < 0.05$).

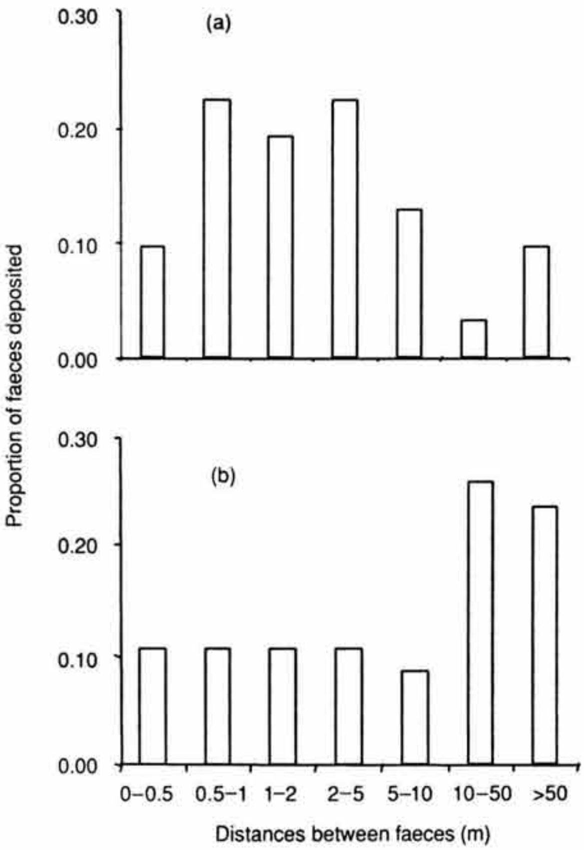

Figure 1. Proportion of faeces deposited by *Alouatta* (a) and *Cebus* (b) at different ranges of distances: n = 31 and 47 for *Alouatta* and *Cebus*, respectively.

Effect of seed dispersal patterns and faecal identity on seed removal

The proportional hazards model showed no effect of the identity of faecal material on the probability of seed removal ($\chi^2 = 0.04$, df = 1, P = 0.844; Figure 2a). In contrast, the quantity of faecal material had a marked and significant effect on the probability of seed removal ($\chi^2 = 44.6$, df = 2, $P < 0.0001$; Figure 2b). Seeds in relatively large amounts of faeces had a lower median life expectancy than seeds in the low-quantity treatment. These differences were attributable to the 50-g treatment ($\chi^2 = 7.22$, P = 0.007), because the 5-g treatment was not significantly different from control (no faeces) ($\chi^2 = 0.36$, P = 0.55). The interaction between quantity and identity of faeces was not significant ($\chi^2 = 3.37$, df = 2, P = 0.19). From daily censuses of footprints on sand beds we found that rodents visited more than 80% of sites.

DISCUSSION

Seed dispersal by white-faced and howler monkeys

The two species of primate studied here can be considered 'opportunistic' or 'non-restricted' frugivores because fruits do not represent the main bulk of their diet. It has been hypothesized that non-restricted frugivores, as a group, produce similar ecological and evolutionary

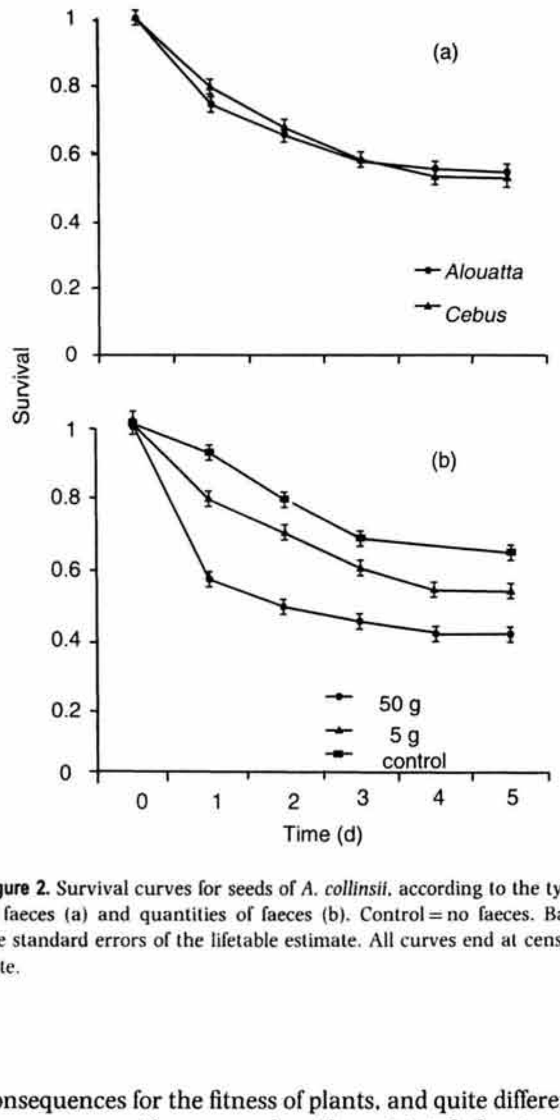

Figure 2. Survival curves for seeds of *A. collinsii*, according to the type of faeces (a) and quantities of faeces (b). Control = no faeces. Bars are standard errors of the lifetable estimate. All curves end at census date.

consequences for the fitness of plants, and quite different consequences if compared with restricted frugivores (Fleming *et al.* 1993, Howe 1993). Here we showed that the short-term ecological consequences for seeds swallowed by two non-restricted frugivores can be completely different. Both *Alouatta* and *Cebus* play an important role as seed dispersers for many tree species in tropical dry forests (Chapman 1989). However, as revealed by this study, there are many aspects in which the dispersal services they provide differ. The contrasting defecation patterns of *Alouatta* and *Cebus* are the result of the different dietary strategies of these two monkey species (feeding behaviour, digestive physiology), and these patterns have a marked effect on the short-term survival of dispersed seeds. Although one of the commonly established requirements for considering a seed dispersal agent as effective is the quantity of seeds dispersed (Chapman & Onderdonk 1998, Stevenson 2000), the quality of seed dispersal may change the final fate of seeds (Schupp 2002).

Alouatta live in cohesive groups that commonly use fruiting trees that offer crops large enough to feed the whole troop, and spend a relatively long time resting in trees. Before moving to another tree, all or most of the individuals defecate more-or-less simultaneously, and this behaviour occurs approximately twice a day. Thus, they produce high amounts of faeces per defecation area (> 250 g inside an area of 2–5 m in diameter). Because of their slow digestive rate, 60% of defecations of a focal troop occur under their sleeping sites (Chapman 1989, Howe 1980, Julliot 1997). Therefore, it is very common that *Alouatta* concentrate high numbers of seeds under their main sleeping sites (Julliot 1996a, 1997). Reported mean dispersal distances of *Alouatta* range between 94–262 m (Estrada & Coates-Estrada 1984, Julliot 1996a, 1997). On the other hand, the feeding groups of *Cebus* (the number of animals feeding in a same tree) vary in size (10–15 individuals per troop), and social relationships inside the group determine which and how many individuals can feed in a tree at the same time (Janson 1990a, b). This forces subordinate individuals to forage on trees with small crop sizes, thus increasing the number of dispersed plant species. As a result, *Cebus* have a broad diet, spend a short time in each tree and travel about 4 km d^{-1}, moving seeds appreciable distances away from the parent plant and depositing them in a scattered pattern. Compared with other sympatric primate species, *Cebus* has short gut retention times (*A. palliata*: 20.4 h, *Ateles geoffroyi*: 4.4 h, *Cebus* sp.: 1.7 h) (Milton 1984, Wehncke *et al.* 2003). This results in higher rates of defecation per day and fewer seeds per faeces.

Effect of seed dispersal patterns and faecal characteristics on seed removal

Results from our experiment showed that the amount of dung is an important factor in determining the short-term removal of seeds and are in accordance with the results of Andresen (2002) and Zhang & Wang (1995). Seeds embedded in relative large quantities of faeces had a higher probability of removal than seeds in small quantities and without faeces. We are confident that most of the seed removal we observed may be attributed to rodents. Dung beetles were not active during the study period (dry season) (Janzen 1983a), and rodent activity was frequently recorded in all the experimental sites (footprints in sand beds placed around experimental sites; E. W. and C. N., pers. obs.). Janzen (1971) and Zhang & Wang (1995) pointed out that seeds removed by terrestrial rodents often represent seed predation, particularly when resources are scarce. In another study, Forget *et al.* (2002) through an annually based model for hoarding in neotropical forests, stated that during the period of low availability of fruit, predation surpasses hoarding (ratio hoarding/predation < 1). Consequently, we think that all the *A. collinsii* seeds that were removed in this experiment were destroyed. This result is in accordance with other studies that have shown that rodents are attracted to sites with relatively high concentrations of faecal material (Andresen 1999, 2001; Chapman 1989, Estrada & Coates-Estrada 1991, Janzen 1982a, Shepherd & Chapman 1998). However, we cannot disregard the possibility that some seeds could escape predation and survive in the seed bank after secondary dispersal.

Seeds in the small quantity of faeces and control treatments had a 38% increase in their short-term survival in comparison with seeds in the large-quantity treatment. This result suggests that a scattered pattern of defecation of small quantities of faeces produce the better conditions for the short-term survival of dispersed seeds. It also underlines the importance of the quality component of seed dispersal and that of the patterns of defecation produced by different dispersers. Nonetheless, our results contrast with those of Andresen (2002), since she concluded that seeds embedded in relatively large quantities of faeces had higher probabilities of seedling establishment than those in small amounts of dung. Large dung piles attracted more dung beetles, which in turn collected and buried more seeds from these piles than from smaller ones. However, because Andresen (2002) did not report the probability of predation associated with the amount of dung, and since she evaluated the effects of rodents and dung beetles in independent experiments, it is not possible to determine whether or not the positive effect of dung beetles overcomes the negative effect of rodents.

Our results indicate that the variation in the defecation patterns produced by different primate species may play an important role in determining seed fate. Furthermore, the discrepancy between the results of Andresen (2002) and ours highlights the dynamic nature of the seed dispersal process. Finally, it is worth mentioning that the dispersal quality provided by any given animal is not constant, but could depend on the particular ecological scenario where dispersal occurs.

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Appendix I. Principal fruit species in the diet of *Cebus capucinus* and *Alouatta palliata*, during the study. Overlap in food plants by the two species of monkey = 30%.

		Seed handling		Seed defecated	
Family	Species	*Alouatta*	*Cebus*	*Alouatta*	*Cebus*
Anacardiaceae	*Spondias mombin*	sw	sp	i	no
Anacardiaceae	*Spondias purpurea*	sw	sp	i	no
Apocynaceae	*Stemmadenia obovata*	sw	sw	no	i
Boraginaceae	*Cordia dentata*	sw	sw	i	i
Bromeliaceae	*Bromelia pinguin*	no	sw	no	i
Burseraceae	*Bursera simaruba*	no	dr	no	no
Capparidaceae	*Capparis baducca*	no	sw	no	i
Capparidaceae	*Capparis indica*	no	sw	no	i
Cucurbitaceae	*Cayaponia attenuata*	no	sw	no	nd
Ebenaceae	*Diospyros nicaraguensis*	no	sw	no	i
Flacourtiaceae	*Casearia tremula*	no	sw	no	i
Fabaceae/Mimos	*Samanea saman*	sw	sp	i	no
Fabaceae/Mimos	*Acacia collinsii*	no	sw	no	i
Fabaceae/Mimos	*Pithecellobium oblongum*	no	sw	no	i
Meliaceae	*Trichilia martiana*	no	sw	no	i
Minispermaceae	*Hyperbaena tonduzii*	no	sw	no	i
Moraceae	*Brosimum alicastrum*	sw	sp	i	no
Moraceae	*Maclura tinctoria*	sw	sw	i	i
Moraceae	*Ficus nitida*	sw	sw	i	i
Moraceae	*Ficus cotinifolia*	sw	sw	i	i
Olacaceae	*Ximenia americana*	no	sw	no	i
Passifloraceae	*Passiflora platyloba*	no	sw	no	i
Piperaceae	*Piper tuberculatum*	no	sw	no	i
Polygonaceae	*Coccoloba* sp.	no	sw	no	i
Rubiaceae	*Guettarda macrosperma*	no	sp	no	no
Sapindaceae	*Paullinia pinnata*	no	sw	no	i
Sapindaceae	*Allophylus occidentalis*	no	sw	no	i
Tiliaceae	*Muntingia calabura*	no	sw	no	i
Viscaceae	*Phoradendron dipterum*	no	sw	no	i
Vitaceae	*Cissus alata*	no	sw	no	i

sw, swallowed; sp, spat out; dr, dropped; i, intact; nd, no data; no, not consumed. For botanical nomenclature see Chavarria *et al.* (2001).

APPENDIX II

Fruit and seed characteristics of the principal species in the diet of *Cebus capucinus* and *Alouatta palliata*, during the study.

Spondias mombin (yellow ellipsoid drupe 1.5–3.5 cm, single seed 2.4 ± 0.45 cm), *Spondias purpurea* (red ellipsoid drupe 2.6 cm, single seed 2.1 ± 0.1 cm), *Stemmadenia obovata* (green round capsule 7–10 cm, orange aril, numerous seeds 0.8 ± 0.09 cm), *Cordia dentata* (white round fleshy drupe > 1 cm, single seed 1.05 ± 0.1 cm), *Bromelia pinguin* (yellow round berry 2–3 cm, 5–15 seeds 0.3–0.4 cm diameter), *Bursera simaruba* (dehiscent trigonal capsule 0.1–0.15 cm, white-orange aril, single seed 0.7 ± 0.04 cm), *Capparis baduca* (brown-scarlet capsule 10 × 1 cm, 5 seeds), *Capparis indica* (brownish long-narrow dehiscent legume > 8 cm, red aril, 3–6 seeds 0.9 ± 0.3 cm), *Cayaponia attenuata* (green-orange round berry 1.1 cm, 1–2 seeds 0.8 ± 0.1 cm), *Diospyros nicaraguensis* (brown-orange round berry 1.9 cm, 1–2 seeds 1.1 ± 0.1 cm), *Casearia tremula* (red-orange capsule 2–3 cm, yellow inside, seed no data), *Samanea saman* (brown-redish flat legume 18.4 cm, 5–10 seeds 1.02 ± 0.1 cm), *Acacia collinsii* (brown flat legume 3.2 cm, yellow aril, 2–5 seeds 0.5 ± 0.1 cm), *Pithecellobium oblongum* (red legume 14–16 cm, white aril, 4–6 seeds 0.8 ± 0.1 cm), *Trichilia martiana* (green capsule 1–1.5 cm, yellow aril, 2 seeds 1.15 ± 0.4 cm), *Hyperbaena tonduzii* (green subglobose drupe 1–1.5 cm, single seed 2.5 ± 0.1 cm), *Brosimum alicastrum* (greenish round drupe > 1.5 cm, single seed 1.5 ± 0.2 cm), *Maclura tinctoria* (greenish round berry > 1 cm, numerous seeds 0.3 ± 0.02 cm), *Ficus nitida* (greenish round syconium > 1 cm, numerous seeds 0.01 cm), *Ficus cotinifolia* (greenish round syconium, numerous seeds < 0.3 cm), *Ximenia americana* (yellow round drupe 1.9 cm, single seed 1.5 ± 0.1 cm), *Passiflora platyloba* (yellow round-fleshy berry > 5 cm, numerous seeds 0.4 ± 0.03 cm), *Piper tuberculatum* (white berry infructescence, numerous seeds < 0.3 cm), *Coccoloba* sp. (pink round drupe 0.6 cm, single seed 0.5 ± 0.05 cm), *Guettarda macrosperma* (green-pink globose berry > 1.5 cm, 1–2 seeds 0.9 ± 0.3 cm), *Paullinia pinnata* (red long-narrow capsule 1.5–2 cm, white aril, single seed > 1 cm), *Allophylus occidentalis* (red globose drupe < 1 cm, single seed 0.6 ± 0.04 cm), *Muntingia calabura* (dark red round berry 1.1 cm, numerous seeds < 0.3 cm), *Phoradendron dipterum* (white-orange round drupe 0.5 cm, single seed), *Cissus alata* (black-dark purple round berry > 0.5 cm, numerous seeds).

II 3. Patrones de dispersión de semillas producidos por monos cara-blanca: implicaciones en la limitación de la dispersión de especies de árboles neotropicales.

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Seed dispersal patterns produced by white-faced monkeys: implications for the dispersal limitation of neotropical tree species

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Summary

1 Primate frugivores are important seed dispersers for a large fraction of tree species in many tropical forests. The movement, diet preferences and defecation patterns produced by primates may therefore strongly influence seed dispersion patterns and seedling recruitment success. Here we examine the pattern of seed dispersal generated by white-faced monkeys (*Cebus capucinus*) in relation to adult tree distribution in the 50-ha plot on Barro Colorado Island (BCI), Panamá.

2 Diet breadth of *Cebus* was remarkably wide. Over four months they consumed fruits of 95 out of an estimated 240 species available. Seeds of 67 species passed intact through the gut and 28 were spat out.

3 Dispersal effectiveness of *Cebus* was also high. Two *Cebus* groups on average spent < 10 min feeding in individual trees, had large home ranges (> 150 ha), travelled 1–3 km day^{-1} and defecated seeds in small clumps throughout the day.

4 Mean dispersal distance of ingested seeds was 216 m (range 20–844 m), with the highest probability of dispersal 100–200 m from the parent plant. For six of nine species studied, the distance between defecation sites and nearest conspecific adults of seeds in faeces was not significantly different from random expectations.

5 The scattered dispersal pattern produced by *Cebus* suggests that this species contributes relatively little to dispersal limitation (*sensu* Nathan & Muller-Landau 2000) compared to other dispersers in the community. Long-distance dispersal by *Cebus* resulted in substantial movement of seeds in and out of the 50 ha plot, and suggests that inverse modelling procedures to estimate dispersal functions from trap data may not adequately describe dispersal patterns generated by this primate.

Key-words: *Cebus capucinus*, dispersal effectiveness, primate dispersal, recruitment limitation, seed dispersal.

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Introduction

Effective seed dispersal is critical to successful recruitment in tropical forests. Dispersal provides the opportunity to escape the neighbourhood of the parent plant, and allows seeds to colonize new and potentially more favourable microsites for seedling establishment (Howe & Smallwood 1982). Neighbourhood effects on recruitment result from the increased risk of mortality to seeds or seedlings from a range of sources including pathogens (Burdon & Chilvers 1982; Augspurger 1983, 1984; Gilbert & De Steven 1996; Dalling *et al.* 1998; Packer & Clay 2000), seed predators (Howe & Primack 1975; Janzen *et al.* 1976; Wright 1983; Clark & Clark 1984; Ramírez & Arroyo 1987; Forget 1993) and herbivores (Condit *et al.* 1992; Barone 1996; Coley & Barone 1996). In one community, these mortality agents have been shown collectively to exert negative density-dependent

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effects on seedling recruitment for every one of 53 species examined in detail (Harms *et al.* 2000). Microsite limitation is likely to be particularly important for small-seeded and light-demanding species (Dalling & Hubbell 2002), but may also be significant for larger seeded, shade-tolerant species with topographically determined habitat requirements (Webb & Peart 2000; Harms *et al.* 2001).

Dispersal success, however, is constrained by the level of resources available for investment in reproduction, and by the effectiveness of seed dispersal agents. At the community level, dispersal success, measured as the proportion of potential recruitment sites receiving seeds of a given species, has been shown to be extremely low for most species (Hubbell *et al.* 1999). As a consequence, dispersal limitation may be a potentially important mechanism for the maintenance of diversity by greatly slowing the local extinction rate of competitively inferior species (Tilman 1994; Hurtt & Pacala 1995; Wright 2002; but see Webb & Peart 2001).

In tropical forests, up to 90% of trees and understorey shrubs have fleshy fruits adapted to attract animals as seed dispersers (Hladik & Hladik 1969; Van der Pijl 1969; McKey 1975; Howe 1977; Janson 1983; Gautier-Hion *et al.* 1985). The foraging movements and behaviour of frugivorous animals therefore have profound consequences on the spatial distribution of recruits (e.g. Bleher & Bohning-Gaese 2001). Indeed, the deposition of seeds into favourable germination sites depends exclusively on the foraging behaviour of the dispersers, and is therefore largely outside the control of the plant (Wheelwright & Orians 1982; Denslow *et al.* 1986). In turn, foraging behaviour depends at least in part upon abundance and availability of fluctuating food sources, competing species, intra-group relationships and the activity of predators (Janson 1985).

Primates are important agents of seed dispersal for a broad range of tropical tree species (e.g. Lieberman *et al.* 1979; Estrada & Coates-Estrada 1984; Gautier-Hion *et al.* 1985; Garber 1986; Janson *et al.* 1986; Tutin *et al.* 1991; Chapman 1995). However, primate species differ in their dispersal effectiveness depending upon their behaviour, physiology and morphology (Lieberman & Lieberman 1986; Levey 1987; Howe 1989; Zhang & Wang 1995). Capuchin monkeys (*Cebus* spp.) are considered especially effective seed dispersers because of their short feeding bouts per tree, and removal of most ingested seeds away from the source tree (Zhang & Wang 1995). While several studies have examined important aspects of the behaviour, ranging patterns, resource use and seed dispersal by capuchin monkeys (Janson 1985; Chapman 1989; Mitchell 1989), few have analysed defecation patterns from the perspective of the plant (Zhang & Wang 1995). Because capuchins defecate seeds in smaller clumps than do most larger-bodied primates (e.g. *C. capucinus* defecation mass: 7.6 ± 4.8 g, $n = 55$; *Alouatta palliata*: 21.1 ± 16.9 g, $n = 35$; E. V. Wehncke *et al.* unpublished data), survival of capuchin-dispersed seeds is likely to be higher relative to other primate species (Zhang & Wang 1995). As with other frugivores, the seed shadows generated by primates may be estimated by combining information on movements and gut passage rates of seeds (e.g. Murray 1988; Holbrook & Smith 2000). However, to characterize the biotic neighbourhood of dispersed seeds at scales relevant to plant recruitment patterns requires detailed information on the distribution of plant species. These data are available from the 50-ha Forest Dynamics Plot on Barro Colorado Island (BCI), Panamá.

Here we assess the seed dispersal pattern generated by the white-faced capuchin, *Cebus capucinus*, and its potential contribution to seedling recruitment on BCI. Specifically, our objectives were to:

1 Determine the dietary preferences and feeding range of *Cebus* groups that forage within the 50-ha Forest Dynamics Plot.

2 Determine the distances and biotic neighbourhoods to which seeds are dispersed.

3 Evaluate the contribution of *Cebus* to dispersal limitation, defined as the reduction in dispersal success resulting from non-random deposition of seeds (Nathan & Muller-Landau 2000).

Materials and methods

STUDY AREA

The study was carried out in a seasonally moist tropical forest on Barro Colorado Island (BCI), Panamá (9°10′ N, 79°51′ W). The island extends over 15.6 km^2 and is covered with tropical moist, semi-deciduous forest of several successional stages (Croat 1978; Foster & Brokaw 1982). Rainfall averages 2600 mm $year^{-1}$ with a seasonal dry period from January until April (Windsor 1990). The annual temperature averages 27 °C, with a diurnal variation of 9 °C. The main part of the study was carried out in old growth forest in the 50-ha Forest Dynamics Plot, on the central plateau of BCI. The plot was established in 1982, and has been censused every 5 years since 1985. All trees > 1 cm d.b.h. have been mapped, tagged and measured. The plot has been described in detail by Condit (1998).

Study species

Cebus capucinus (white-faced monkeys) are relatively small primates weighing on average 3 kg (Milton 1984) and ranging from Honduras to Ecuador (Wolfheim 1983). Previous work on *C. capucinus* on BCI has shown that the bulk of its diet (65%) is made up of fruit and that group movements are related to the location of fruit sources (Hladik & Hladik 1969; Mitchell 1989). *Cebus* live in permanent social groups ranging from 5 to 24 individuals (Oppenheimer 1968; Mitchell 1989). According to Mitchell (1989) at least 16 groups live on BCI, with an estimated total population of between 278 and 313 individuals. Home ranges average

90 ± 13.2 ha, $n = 4$ (Mitchell 1989). In addition to *C. capucinus*, howler monkeys (*Alouatta palliata*), tamarins (*Saguinus geoffroyi*), night monkeys (*Aotus trivirgatus*) and a single, re-introduced group of spider monkeys (*Ateles geoffroyi*) are present on BCI.

RANGE SIZE AND RANGE USE

Two groups of *Cebus capucinus* (hereafter *Cebus*) were followed around the central plateau of mostly old-growth forest on BCI. The groups contained 15–17 individuals, and their home ranges overlapped in and near the 50 ha plot. The study was carried out over four months (March–July 1999) at the end of the dry season and the transition to the wet season, when most plant species fruit (Foster & Brokaw 1982). The groups were observed during a total of 180 h. Observations were more or less evenly distributed across all hours of the day (from 6:00 to 18:00 h). Identifying marks on individual faces allowed us easily to track the same groups. Each group was followed separately, and its location was recorded every 10 min, or when abrupt changes in the direction of travel occurred. Locations within the plot were determined by recording the tag number of the closest tree. Outside the plot, locations from either trails or the plot edge were estimated using a compass and pedometer. Although *Cebus* individuals commonly move together as a group, intra-group spatial positions tend to differ according to individual social status (Janson 1990a,b). Therefore for calculations of feeding bouts per tree, peripheral subordinate individuals were not considered members of the group. We estimated the time of entry/exit from feeding trees as those times when the first non-peripheral individual monkey of the group started and the time when the last non-peripheral individual finished feeding in each tree.

We used the program TRACKER™ (Version 1.1, Solna, Sweden) to calculate the home range (area traversed by a group during a given period) and feeding area (locations where the monkeys search for and eat fruits) of each *Cebus* group. The Minimum Convex Polygon method was used to calculate the size of the home range. This method is frequently used in home range studies (e.g. Mohr 1947; Thies 1998; Holbrook & Smith 2000), and works particularly well for animals that move together in groups. Using this method, isopleths are generated that connect the outermost coordinates in the range with the same estimated density of observations. The technique provides a non-parametric mapping method that can be applied to autocorrelated points (the most common case for tracking data).

DIET AND FEEDING PATTERNS

Diet was characterized from observations of feeding events and from analysis of faecal material. We recorded the location and time spent feeding by the group (as defined above) in each fruiting tree, and collected a sample of the fruit, seed or other plant part eaten for later identification. In addition, we recorded how seeds were handled (seeds spat out, seeds damaged and seeds swallowed) by classifying how the majority of seeds per species were treated by the monkeys.

We used the Kernel method within TRACKER to define feeding areas (Worton 1989; Seaman & Powell 1996). With this method, a feeding probability density function is fitted around each mapped feeding observation. Isopleths of equal estimated feeding probability are generated by superimposing a grid over the observed data and estimating feeding probability densities at each grid intersection. The kernel density estimator has the desirable qualities of directly producing a density estimate, and being uninfluenced by effects of grid size and placement (Silverman 1986). Using TRACKER, isopleths can be generated enclosing any percentage of feeding events. For this study we used isopleths enclosing 95% of feeding observations. We chose a time interval of 10 min between feeding observations to define feeding areas. Finally, we measured the areas enclosed by the isopleths selected.

To evaluate whether the estimated feeding range of *Cebus* corresponded to an area of high abundance of preferred fruit trees, we compared the abundance of preferred adult (reproductive-sized) trees per ha inside the feeding range and outside the feeding range but within the plot, and between the overlap and non-overlap areas of the feeding ranges of the two groups. Preferred fruit species were defined as those that contributed > 5% of the total time *Cebus* spent feeding ($n = 6$ species).

DEFECATION AND SEED DISPERSAL

Where possible, defecations were collected while following the monkeys. The samples were taken to the laboratory and all seeds found were counted and identified. The number of seeds < 1 mm long was estimated from counts made of weighed subsamples of faecal material. We mapped every location where faeces were dropped, and recorded the tag number of the nearest-neighbour plant for defecations inside the 50-ha plot.

With *Cebus* it is practically impossible to follow the same individual for prolonged periods. Therefore, to obtain valid seed dispersal distances, we first needed to measure the monkey's seed retention time. We did this by feeding five captive *Cebus* at the Summit Zoo, Panamá, with four different cultivated fruit species varying in seed mass (melon, papaya, cucumber and tomato; range in fresh seed mass: 0.002–0.13 g, length: 3.3–17.1 mm, width: 2.4–6.3 mm), on five consecutive days. The average time for > 75% of seeds to appear in faeces was 105 ± SD 38 min ($n = 36$) (E. V. Wehncke unpublished data). There were no significant effects of individual *Cebus* or seed type on gut retention time ($F_{7,33} = 1.58$, $P = 0.17$). To verify whether gut passage times from captive monkeys are representative of wild monkeys, we also directly calculated gut passage times from our records of feeding events on infrequently consumed species and from the subsequent collection of faecal samples in the field. These passage times for wild monkeys corresponded closely to our data from the captive population (mean = 94 ± 43 min, $n = 33$). We therefore selected 100 min for all calculations of seed dispersal distances as it represents an intermediate value between seed passage times of captive and wild *Cebus*. This estimated passage time of 100 min was also found in a study of captive *Cebus apella* in Brazil (E. V. Wehncke unpublished data).

Data on gut passage time, the location and time of departure from feeding trees, and subsequent movement patterns were used to calculate seed dispersal distances. Trees considered for analysis were those in which monkeys spent more than 5 min feeding on fruits and which had seed sizes that fall in the range of swallowed seeds. From information on the location of groups and on the time spent feeding per tree visited we calculated the probability of movement away from the food tree prior to defecation. The time of exit from feeding trees was estimated as the time when the last individual of a group left each tree. To evaluate the probability with which *Cebus* defecated seeds beneath conspecifics we used 26 days of tracking data and a sample of 428 trees to estimate the probability of visiting a conspecific tree after the mean time of seed transit through the gut (100 min). To estimate the proportion of feeding events resulting in seed movement inside and outside the plot, we used data of the position of feeding trees and of the estimated position of the group at defecation and counted the events occurring inside and outside the plot.

Finally, we evaluate whether *Cebus* preferences for particular fruits results in shorter than expected dispersal distances. For the nine species most abundant in faeces we compared the mean distance between seed defecation sites and the nearest adult conspecifics with the mean distance between 100 sites within the plot chosen at random and nearest adult conspecifics. As distances between trees and random plot locations were not normally distributed we used the one-tailed Mann–Whitney *U*-test for the comparison of each species. Seeds in defecations and random points found nearer a plot boundary than an adult conspecific have been excluded from the analyses.

Results

RANGE SIZE AND RANGE USE

Two *Cebus* groups, and on a few occasions some solitary individuals (that could have been members of these groups), were seen feeding inside the plot. Both groups of monkeys moved approximately 1.5–3.5 km each day. Group 1 was followed inside and outside the plot, whereas Group 2 was followed only inside the plot, although its range extended beyond the plot. The home range of group 1 occupied *c.* 150 ha (inside plot: 41 ha, $n = 437$ points; outside plot: 109 ha, $n = 522$ points). The 50-ha plot therefore comprised 27% of the total home range of this group. Group 2 used an area of 33 ha inside the plot ($n = 249$ points). Therefore, group 1 used 81% and group 2 used 67% of the plot. Considering that their estimated home-range overlap inside the plot is 31 ha ($n = 17$ points), we calculated that both groups together used 86% of the plot (43 ha).

Considering both groups together, a total of 39 ha inside the plot were used for feeding (78%). Separately, group 1 used 29 ha and group 2 used 32 ha of the plot for feeding. The overlap in their feeding area was of 22 ha (44% of the plot, $n = 172$ points). We found no clear evidence to suggest that the within-plot feeding range of *Cebus* was determined by a higher availability of preferred tree species. Considering only the six most frequently consumed species, we found a greater density of adult trees outside (71.9 trees ha^{-1}) rather than inside this feeding area (45.5 trees ha^{-1}). However, the density of adult trees where feeding ranges overlapped was higher (53.9 trees ha^{-1}) than in the rest of their feeding area (21 trees ha^{-1}).

DIET

Cebus monkeys spent 53% of the total observation time feeding on fruits (5652 of 10630 min) and on average spent 9.1 ± 6.8 min (range 1–52 min; $n = 624$) feeding per fruiting tree. Over the 4 months of the study the two groups manipulated fruits of 105 species, and ate all but 10 of them (Appendix 1). These 10 species were opened and seeds removed while looking for insects. Of the 95 species eaten, the seeds of 67 of them were swallowed and passed intact through the gut, and 28 were spat out. Seeds eaten by *Cebus* ranged from 0.1 to 7 cm long, and seed sizes swallowed were between 0.1 and 3 cm long (Appendix 1). From several sources of information we estimated that 240 species of trees, shrubs and lianas fruited within the study area (J. Wright, R. Perez, R. Foster, unpublished data). Therefore, we estimate that 40% and 28% of species in fruit were consumed and swallowed, respectively.

We estimated that a *Cebus* individual produces 8–10 defecations per day. On average, fresh faeces weighed 7.6 ± 3.2 g ($n = 9$). Ninety three percent (161 of 174) of faecal samples collected contained seeds, which in total represented 67 species. Each dropping contained on average 2 ± 1.3 (range 0–8) different seed species. Small-seeded (< 3 mm length) species were present in most of the faecal samples collected (seeds of *Cecropia* and *Ficus* were present in 90% of the seed containing faeces). Faeces that contained only *C. insignis* seeds contained on average 1430 ± 700 seeds ($n = 9$). By contrast the top six species (those representing the most abundant species in faeces, with seeds > 3 mm length) occurred in droppings at densities of 7–57 seeds per dropping (average numbers of seeds per droppings: *Havetiopsis flexilis* = 56.9 ± 155.5, $n = 21$; *Laetia procera* = 29 ± 16.6, $n = 11$; *Randia armata* = 11.2 ± 12.8, $n = 13$; *Cordia bicolor* = 4.3 ± 4.7, $n = 26$;

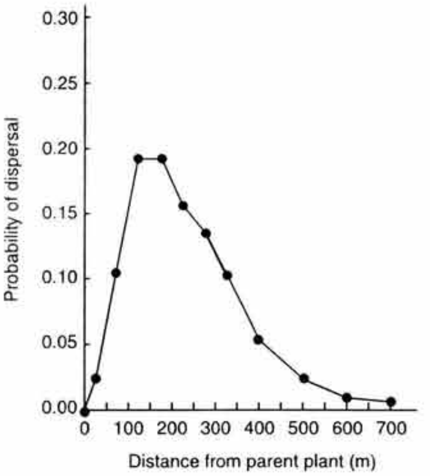

Fig. 1 Probability of seed dispersal by *Cebus* away from a parent plant. Estimates are based on individuals inside and outside the 50-ha plot.

C. lasiocalyx = 4.4 ± 2.9, and $n = 20$; *Hasseltia floribunda* = 6.9 ± 9.3, $n = 7$).

MOVEMENT PATTERNS AND SEED DISPERSAL DISTANCE

In general, the distance travelled by *Cebus* was also a good predictor of the dispersal distance, because the routes from one tree to the other tended to follow straight lines. The two groups visited 624 trees, at a rate of 3.1 ± 1.3 trees h^{-1} and 1.6 ± 0.9 species h^{-1}. Seeds < 3 cm in length were typically swallowed along with the attached fruit pulp. Fruits with seeds too large to be swallowed and most unripe fruits (8.6% of the species handled) were dropped under the tree or up to 20 m from the source. *Cebus* moved swallowed seeds from 10 m to 844 m away from parent plants, with the highest probability of seed dispersal ranging between 100 m and 200 m (Fig. 1), and a mean distance of seed travel of 216 ± 121 m ($n = 323$). For seeds consumed inside the plot, where locations could be more accurately determined, we found an average dispersal distance of swallowed seeds of 208 ± 113 m (range: 20–844 m, $n = 170$). Although we found that seed size did not affect gut passage time for captive *Cebus*, variation in the spatial location of fruit trees and in the time spent feeding and manipulating fruits might result in differences in dispersal distances among species. We found the highest estimated distance for *Pterocarpus rohrii* (843.8 m), followed by *Capparis frondosa* (334.7 m) and *Paullinia bracteosa* (334.7 m), and the lowest for *Apeiba membranacea* (61.6 m).

Dispersal by *Cebus* resulted in a high flux of seeds in and out of the plot. Overall, 26% of feeding events inside the plot resulted in dispersal beyond its perimeter ($n = 223$). As expected, fewer feeding events recorded outside the plot resulted in dispersal into it (8%, $n = 153$). All of the tree species dispersed into the plot were already represented there as recruits > 1 cm d.b.h.

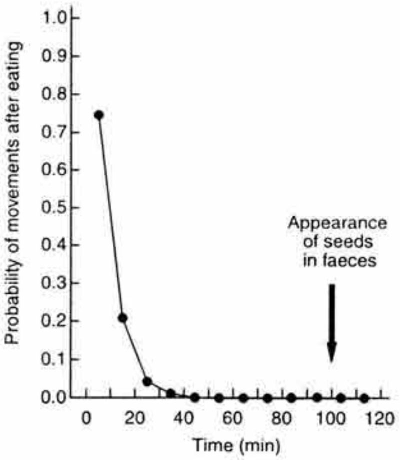

Fig. 2 Probability of movement of *Cebus* away from fruiting trees after starting feeding.

DEPOSITION SITES AND BIOTIC NEIGHBOURHOOD

Once feeding bouts started in a tree, the highest probability of group movement away from that tree was within the following 10 min (Fig. 2). Therefore, *Cebus* monkeys almost always moved seeds that they swallowed away from the crown of the maternal tree. Sequential selective foraging on favoured species, however, could result in dispersal back below or near conspecifics. We evaluated this possibility in several ways. Firstly, we compared the identity of trees where defecations occurred with their seed contents. Only 7 of 138 defecations examined were deposited beneath conspecifics. Secondly, we used tracking data to calculate the probability that *Cebus* would visit a conspecific after the mean time of seed transit through the gut. For a sample of 428 trees this probability was only 0.093. Thirdly, we compared the mean distance between defecation sites and nearest adult conspecifics with the mean distance to nearest adult conspecifics if seeds were deposited at random through the plot. We found that for six of nine species present in 161 defecations, mean distances from random points and from defecation sites were not significantly different (Table 1). For the remaining three species, distance to conspecifics from defecation sites was significantly shorter than expected. Two of these species, *Cecropia insignis* and *Cordia bicolor*, were among the most frequently visited by *Cebus* (Appendix 1), yet differences in mean distance were rather small (< 10 m). The remaining species, *Ficus costaricana* is represented by only seven adults in the plot, only one of which was visited by *Cebus* and may have been the only individual that was reproductive during the study period.

Discussion

Our results indicate that *Cebus capucinus* monkeys on BCI are effective seed dispersers that are likely to strongly influence the recruitment success of trees

Table 1 Average minimum distances within the plot between (i) 100 randomly selected points and the nearest reproductive-sized tree of each species listed, and (ii) defecation locations and the nearest reproductive-sized conspecific tree. Differences in distance distributions are tested with the Mann–Whitney *U*-test

	Minimum distance (random points)		Minimum distance (defecation sites)					
Species	Mean (m)	SD	Mean (m)	SD	Reproductive trees (N)	Defecation sites (N)	*U*	*P*
Cecropia insignis	48.87	31.24	41.67	37.35	112	55	2209	0.04
Cordia bicolor	29.95	19.50	21.56	15.45	234	22	811	0.05
Desmopsis panamensis	7.13	4.84	3.86	172.55	3249	4	112	0.14
Ficus costaricana	160.87	93.61	48.93	26.52	7	15	150	< 0.01
Ficus yoponensis	195.61	94.08	208.64	51.11	5	15	712	0.75
Hasseltia floribunda	27.51	18.12	23.61	14.11	254	6	273	0.71
Laetia procera	262.49	184.75	269.19	145.93	28	10	477	0.81
Miconia argentea	52.22	35.49	48.16	50.93	75	14	565	0.24
Randia armata	18.67	11.20	14.19	7.91	481	9	355	0.30

whose seeds they swallow. High dispersal effectiveness results from the following attributes: (i) long-distance and near-continuous daily movement patterns; (ii) a highly frugivorous diet encompassing many species; (iii) scattered deposition of seeds through frequent defecations; (iv) inferred low rates of post-dispersal seed predation relative to other primate species. Below we discuss these attributes of dispersal effectiveness in more detail.

RANGE USE AND MOVEMENT PATTERNS

We recorded daily movement patterns of up to 3.5 km by the two groups of *Cebus* studied on BCI. This is comparable with observations made by Zhang & Wang (1995) of *C. apella* in French Guiana (about 2 km day^{-1}). Both groups on BCI used the 50-ha plot during the study, feeding in 67–86% of the total plot area. The groups overlapped in their feeding area over almost half of the plot. Assuming that *Cebus* monkeys move in relation to the location of preferred available fruit sources (Hladik & Hladik 1969; Mitchell 1989), such a strong overlap of feeding areas may suggest a high concentration of preferred species in that area. We found no evidence for increased densities of preferred fruit trees inside the feeding area compared with the rest of the plot, although a larger proportion of trees may have been in fruit in the feeding range, or may have produced larger fruit crops.

However we would expect the distribution of reproductive trees to have only a relatively diffuse effect on foraging locations during the dry–wet season transition, given the tremendous diet breadth of this primate species, which consumed 40% of all species in fruit available during the study. Rather than tracking the distribution of fruiting trees, *Cebus* movement patterns may be a consequence of other factors, including intraspecific competition, predation pressure (if existent in the study site) and the distribution of food resources other than fruit (e.g. invertebrate and vertebrate prey and water holes).

EFFECTIVENESS OF DISPERSAL BY *CEBUS*

Despite the short duration of the study, the two *Cebus* groups manipulated and consumed 105 species of fruit from inside and outside the 50-ha plot. In addition, the seeds of a majority of them (64% of 95 fruit species consumed) were found intact in their faeces. Three factors may help explain the diversity of the *Cebus* diet. First, the study was carried out at the dry–wet season transition when most of tree species on the island fruit (Foster 1982). Second, the social organization of the *Cebus* group influences feeding behaviour because members with low dominance rank avoid entering trees with low fruit production until after the rest of the group has left (Janson 1985; E. V. Wehncke pers. obs.). In the meantime, they remain in surrounding trees exploring for new food items. Third, Milton (1984) suggested that food choice might be dictated as much by internal constraints intrinsic to the digestive physiology of the feeder as by extrinsic factors such as nutrient content or relative availability. *Cebus* turned over gut contents very rapidly, and this fast food passage permits them to rid the gut rapidly of indigestible seeds present in fruit. Consequently, *Cebus* are able to compensate for the low protein content of some foods by turning over a large volume of fruit each day (Milton 1984).

QUALITY OF *CEBUS* SEED DISPERSAL

Characteristics related to morphology and physiology of *Cebus* also explain the effectiveness with which these seeds were dispersed. Dispersal effectiveness is defined as the contribution a disperser makes to the reproductive success of a plant, and is determined by the quantity of dispersed seeds and the quality by which seeds are dispersed (Schupp 1993, 2002). In turn, the quality of seed dispersal can be characterized by the treatment that seeds receive by the disperser and the spatial pattern in which they are deposited (Schupp 1993, 2002). We show here that the gut retention times for *Cebus* (100 min) is much shorter than for other sympatric primate species (*Alouatta palliata*: 20.4 h, *Ateles geoffroyi*: 4.4 h, Milton 1984), resulting in more defecation events per day and fewer seeds per dung pile. Furthermore, individual *Cebus* faeces were small and were produced asynchronously by members of the group. Scattered dispersal of small numbers of seeds may strongly influence post-dispersal seed fate for *Cebus* relative to other primates (Howe 1989). Zhang & Wang (1995) showed that in Guyana seeds dispersed by spider monkeys (*Ateles paniscus*) were more than twice as likely to be subsequently removed as seeds dispersed by *Cebus apella*. Similarly, in a tropical dry forest (E. V. Wehncke *et al.* unpublished data) have shown that seed removal by rodents in *Alouatta palliata* (howler monkey) faeces was higher than from *Cebus capucinus* faeces. Because most seed removal is likely to result in seed predation (Janzen 1971), the amount of faecal mass likely has a direct effect on post-dispersal seed survival.

The second component of dispersal effectiveness is the biotic and abiotic neighbourhood into which seeds are dispersed. Dispersal below or close to conspecific crowns is likely to result in lowered probabilities of recruitment due to increased seed and seedling predation (Janzen *et al.* 1976; Augspurger 1983, 1984; Condit *et al.* 1992; Forget 1993; Coley & Barone 1996). Although short seed retention times might be expected to result in defecation of seeds below or close to parent trees, this did not occur. *Cebus* spent a maximum of 50 min foraging in a single tree and most frequently left within 10 min of starting to feed. This resulted in a high rate of trees visited and dispersal distances averaging 216 m.

CONSEQUENCES OF *CEBUS* DISPERSAL FOR RECRUITMENT LIMITATION

One of the major factors thought to contribute to tree species coexistence is the failure of seeds to arrive at potential recruitment sites (Tilman 1994; Hurtt & Pacala 1995; Pacala & Levin 1997; Zobel *et al.* 2000). This phenomenon, called seed limitation, reduces population growth rates and provides a mechanism by which competitively inferior species can be maintained in a community for prolonged periods (Crawley 1990; Turnbull *et al.* 2000; Muller-Landau *et al.* 2002). Seed trapping in tropical forests indicates that some degree of seed limitation, determined either by limited reproductive output (source limitation, *sensu* Nathan & Muller-Landau 2000), or clumped patterns of seed distribution (dispersal limitation, *senso stricto* Nathan & Muller-Landau 2000; Schupp *et al.* 2002) operates for almost all species in the community. This includes very common species and small-seeded species dependent upon the availability of particular microsites (Silman 1996; Hubbell *et al.* 1999; Dalling *et al.* 2002).

Our observations of *Cebus* indicate a tendency of this dispersal agent to contribute relatively little to the overall dispersal limitation of species whose seeds it swallows. The combination of short feeding bouts, a broad diet, rapid movement and asynchronous defecation within the group meant that the locations of seed deposition sites were widely spaced, and were not significantly different from random with respect to distance to nearest adult conspecifics, at least for most species. This contrasts with many other vertebrate frugivores capable of equally long-distance seed dispersal. Important alternate dispersers of species consumed by *Cebus* on BCI include bats, tapirs, and howler and spider monkeys. These frugivores are also capable of moving seeds several hundred metres but are likely to contribute more strongly to dispersal limitation than *Cebus* because seeds are primarily deposited in large clumps at feeding roosts, latrines and sleep trees (Julliot 1986; Zhang & Wang 1995; Fragoso 1997; Thies 1998; Schupp *et al.* 2002).

CONSEQUENCES FOR MODELLING SEED DISPERSAL

Vertebrate frugivores generate dispersal patterns that have proven difficult to describe with current models. Recently, inverse modelling procedures have been developed that use data on the location of adult trees and seed collections in traps to characterize seed dispersal patterns (Ribbens *et al.* 1994; Clark *et al.* 1999). These models hold much promise for characterizing landscape-level seed limitation and for providing an integrated measure of the net activity of all dispersal agents against which the relative effectiveness of particular dispersers could be evaluated (Nathan & Muller-Landau 2000).

The application of inverse modelling on BCI has shown good fits between actual and predicted seed capture to mesh traps arrayed on the 50-ha plot for wind-dispersed species, but rather poorer fits for vertebrate-dispersed species (Dalling *et al.* 2002). Our results indicate that a limitation to applying this technique for primate-dispersed species is that the mean dispersal distance of > 200 m for *Cebus* greatly exceeds the mean distance between reproductive sized conspecifics for most tree species on the plot. A future generation of dispersal predictors will therefore likely require much larger mapped forest stands and more parameter-rich models that can account for the complex movement patterns of vertebrate frugivores.

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Supplementary material

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/JEC/JEC798/JEC798sm.htm

Appendix S1 List of plant species manipulated by *Cepus capucinus* during 4 months.

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CAPÍTULO III

Patrón de dispersión de semillas a larga distancia por monos del género *Cebus* en Iguazú, Argentina: consecuencias para las semillas de *Miconia*

(Artículo en revisión en Journal of Ecology)

Long-distance seed dispersal pattern generated by *Cebus* monkeys in Iguazú, Argentina: consequences for *Miconia* seeds

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Running headline: Long-distance seed dispersal by *Cebus*

Summary

Long-distance seed dispersal may influence many key aspects of plant biology such as the genetic structure of populations, long-distance gene flow, and the colonization of new habitats. In spite of its importance, most empirical efforts have focused on the more affordable study of short-distance dispersal. Here, we integrate the study of the natural seed rain of a focal tree species *Miconia pusilliflora* with the seed dispersal pattern generated by *Cebus apella*, to identify and quantify long-distance dispersal events. We found that *Cebus* monkeys are effective seed dispersers of *Miconia* seeds because a) they moved seeds up to 1,150 m away from parent plants, with the highest probability of dispersal between 300 to 400 m, b) seeds taken far have a greater chance to survive at least up to the seedling stage, c) they dispersed an underestimated number of seeds (the 1% of total seeds observed in traps, annually) to long distances, and what is of critical importance, far of any conspecific tree. In this forest the community of dispersers is not limited only to *Cebus* monkeys, therefore having a better picture of the rate of long-distance seed dispersal events produced by the entire community of dispersers and for a sufficient number of plant species for a particular forest environment would help us to realize that those events probably are more common than expected. Since these types of events are the ones that probably have the highest biological consequences like the colonization of new habitats and/or the homogenization of plant populations, seed dispersal patterns of pioneers should consider vertebrate-long-distance seed dispersal patterns when modelling seed dispersal.

Keywords: *Cebus*, defecation patterns, long-distance seed dispersal, *Miconia*, seed rain.

Introduction

It has long been recognized that seed dispersal has important implications for the growth, reproduction and survival of individuals, for the composition and structure of plant populations and communities, and for the geographical distribution and evolution of species (Tilman & Kareiva 1997, Clobert *et al.* 2001, Nathan 2001). It determines the potential area for plant recruitment (Howe & Smallwood 1982, Dalling & Hubbell 2002) and also contributes to species coexistence by producing a heterogeneous species distribution, thus reducing competitive interactions (Tilman 1994, Hurtt & Pacala 1995, Holmes & Wilson 1998, Wright 2002). Most of these advantages, however, are probably associated with rare, long-distance seed dispersal events that move propagules beyond the influence of the maternal or related plants, as well as to new and potentially colonizable habitats. In spite of the importance of long-distance dispersal, most empirical efforts have focused on the more affordable study of short-distance dispersal (Cain *et al.* 2000). For example, there have been improvements in the estimation of the parameters describing the short-distance dispersal curves of some species (Portnoy & Willson 1993, Ribbens *et al.* 1994, Clark *et al.* 1999, Nathan & Mueller-Landau 2000), but the inherent difficulties associated with the rarity of long-distance seed dispersal have precluded a more thorough study of this phenomenon (Cain *et al.* 2000, Fragoso *et al.* 2003). Yet, long-distance seed dispersal may influence many key aspects of plant biology such as the genetic structure of populations, long-distance gene flow, and the colonization of new mircohabitats (Harper 1977, Sauer 1988, Hengeveld 1989, Hanski & Gilpin 1997, Hovestadt *et al.* 1999).

Long-distance dispersal has caught the attention of modelers in the last few years (Turchin 1998, Clark *et al.* 1999, Higgins & Richardson 1999). This is a consequence of the critical importance that long-distance dispersal events have in the context of habitat fragmentation (Malanson & Armstrong 1996), plant invasions, migration rates (Shaw 1995, Higgins & Richardson 1999, Richardson *et al.* 2000), and genetic differentiation of populations (Le Corre *et al.* 1977). Apparently, mixed models seemed to be the most adequate method for modelling dispersal curves, especially the shape and the extent of the tail (Clark *et al.* 1999, Bullock & Clarke 2000, Nathan & Mueller-Landau 2000). However, captures in seed traps may fail to adequately characterize seed dispersal patterns of pioneers if vertebrate-long-distance seed dispersal patterns are not considered when modelling seed dispersal.

Animal frugivores are one of the potential agents capable of producing long-distance seed dispersal. The influence of vertebrate frugivores goes beyond seed dispersal, since they also affect seedling establishment and the spatial distribution of seedlings and trees (Bleher & Böhning-Gaese 2001, Fragoso *et al.* 2003). Although, vertebrate frugivores generate dispersal patterns difficult to describe with current models (Dalling *et al.* 2002, Wehncke *et al.* 2003), some methodological approaches for quantifying dispersal patterns of zoochorously dispersed seeds (direct measurement of movements of seed disperser organisms, genetic analyses, and mathematical models), can be used to yield realistic estimations by predicting approximate seed dispersal distances. In turn, knowledge of animal behaviour and plant characteristics can be combined to predict long-distance seed dispersal by animals.

Here, we attempt to integrate the study of the natural seed rain of a focal tree species with the seed dispersal pattern generated by a vertebrate frugivore, to identify long-distance dispersal events. In particular our objectives were: 1) to evaluate the effect of *Cebus* on seedling emergence below and away from *Miconia pusilliflora* parent trees; 2) to describe the natural seed shadow of this pioneer tree, by the conventional method of seed traps; 3) to compare the trap-derived seed shadow with the shape of *Miconia* seed shadow generated by the brown capuchin monkey, *Cebus apella*; and 4) to compare the trap-based estimation of the distribution of seed densities with the expected distribution derived from a spatially-explicit simulation. This comparison will allow us to evaluate the frequency of long-distance seed dispersal events.

Methods

STUDY AREA AND SPECIES

The study was carried out in a humid subtropical forest in the Iguazú National Park (60,000 ha in size), Argentina (25°40'S, 54°30'W). Rainfall in the area averages 2000 mm/yr, with a pronounced seasonality in day length and temperature (Crespo 1982, Brown & Zunino 1990). The winter (June-August) is characterized by low temperatures and a relatively low availability of fleshy fruits and arthropods compared to spring and summer (October-March) (Placci *et al.* 1994, Di Bitetti 2001). Therefore, winter is a critical period of fruit scarcity for *Cebus* and other frugivores (Janson & Di Bitetti 1997). Consequently, during the study period (the transition from the less to the most productive season, 29 August to 20 December 1998), *Miconia pusilliflora* (Melastomataceae) (hereafter *Miconia*), was the most heavily consumed fruit by *Cebus.* Seeds appeared in viable condition and in high quantities in faeces (82% of feeding events and 54% of faecal samples corresponded to *Miconia*). During this study, the diet of our *Cebus* focal group was artificially supplemented with bananas (between 16 September and 5 October), as part of provisioning experiments run in the same area (see Di Bitetti 2001). That study had the potential to affect the movements of monkeys; concentrating most of them around the study area of *Miconia* patches (see Di Bitetti 2001).

Miconia pusilliflora, a common pioneer tree species that fruits from August to December in the study area, produces fleshy berries containing an average of 7 small seeds zoochorously dispersed. Mature fruits are of > 3 < 5 mm diameter (average dry weight: 0.04 g). Each seed has an average dry weight of 0.013 g.

Cebus apella, the brown capuchin monkey, ranges from Colombia to northern Argentina occupying a variety of tropical and subtropical forests (Wolfheim 1983). This primate is an omnivore but consumes a high proportion of fruits and insects. It also includes shoots, leaf bases, eggs, and vertebrates in its diet (Terborgh 1983, Robinson & Janson 1987, Brown & Zunino 1990). Previous work on *C. apella* in the Iguazú area and with the same focal group has shown that the abundance and distribution of fruits are the main determinants of home-range use by this monkey (Di Bitetti 2001). *C. apella* lives in social polygamous groups of 7-30 individuals (Di Bitetti 2001) and is the only species of primate living in the Park. In the study area, *C. apella* has an estimated density of 16 individuals per km^2, and it was estimated that this group has a home range of 172 ha, from 91 days of complete follows (Di Bitetti 2001). A trail system covering an area of 6 km^2 and marked at 50 m intervals was used to follow the study group. Capuchin monkeys (*Cebus* spp.) are effective dispersers of species whose seeds they swallow (Wehncke *et al.* 2003). This result from the following attributes: 1) long-distance and near continuous daily movement patterns, 2) scattered deposition of seeds through frequent defecations, and 3) inferred low rates of post-dispersal seed predation (Wehncke *et al.* 2004).

EFFECT OF *CEBUS* ON SEED GERMINATION AND SEEDLING EMERGENCE OF *MICONIA*

To examine the effect of dispersal by *Cebus* on the germination and seedling emergence of *Miconia*, we performed germination experiments in the field. On 9 and 10, October 1998, 160 seeds collected from mature fruits (control) and 160 seeds defecated by monkeys were planted below the crown of a *Miconia* tree, and at 50 m away from this or any reproductive conspecific tree. We established 15 replicates of this treatment with a total of 9,600 seeds planted in the field (640 seeds per replicate). Groups of seeds were incorporated into separate nylon bags containing approximately 3 cm^3 of sterilized soil, and buried at soil surface level. At each burial location, bags were sheltered from the seed rain by a 0.1 mm nylon mesh roof of 60 × 80 cm raised 50 cm above the ground. Emergence of *Miconia* seedlings was measured at weekly intervals until successive censuses showed no change in the number of emerged seedling (last recording date: 22, December 1998). The effect of seed transit through the gut of monkeys and that of dispersal distance on seedling emergence was evaluated by means of an analysis of deviance using the proportion of germinated seeds from the total number planted, the binomial error distribution, and the link function = Logit (SAS Institute, 1999-2001).

SEED SHADOWS OF ISOLATED *MICONIA* TREES

Four isolated reproductive *M. pusilliflora* individuals (trees $\geq$ 5 cm dbh) with approximately the same crown diameter were selected as focal trees to estimate the number of seeds that reached different distances from the parent tree. The focal trees selected represented the mean crop size of the *Miconia* population. We used a linear model to estimate the best function describing the seed shadows for these focal trees. All focal trees were ≥ 50 m away from the nearest reproductive conspecific. In August 1998, four 0.07-m^2 plastic traps were placed at random locations below the crowns of each focal *Miconia* tree. In addition, two 20 m transects were laid out along bearings chosen at random and starting from the projection of the centre point of the crown of each focal tree. On each transect, one 0.07-m^2 plastic trap was placed at 5 m, 10 m, and 20 m away from the crown edge. Censuses were performed at 10 days intervals during the period of fruit production and dispersal (19 August to 10 December). In each census we collected all the fruits and seeds of *M. pusilliflora* present in the traps. We estimated the number of seeds within fruits based on fruit size (see Dalling *et al.* 1998). All fruits were measured with callipers and sorted into two size categories (2-3 mm, median = 5 viable seeds per fruit; > 3 mm, median = 7 viable seeds per fruit). The remaining material was dried in an oven at 40°C and individual seeds were counted under a magnifying glass. Monkeys were never seen to spit out *Miconia* seeds, they always swallowed them. In the study site, we have never found *Cebus* faeces in the traps. Thus, we can exclude *Cebus* dispersal from the estimation of seed shadows of focal trees and assume that we effectively evaluated the dispersal pattern in the absence of monkeys.

FEEDING PATTERNS AND THE *MICONIA* SEED SHADOW GENERATED BY *CEBUS* MONKEYS

To examine the shape of the seed shadow of *M. pusilliflora* produced by *Cebus*, one group of monkeys was followed and observed during 4 months (August - November). From these data we then selected a total of 357 h (10 September-3 November). This period corresponded to the first and last records in which *Cebus* was observed consuming *Miconia* fruits. The location and time spent feeding by the group in each fruiting tree was recorded, and their daily routes were traced onto maps. To estimate the number of *Miconia* seeds in *Cebus* faeces a total of 48 faeces were collected during September, and all seeds of *M. pusilliflora* found were counted and identified. Dispersal distances were estimated directly from maps as the straight line between the feeding trees and the positions of the group after 100 min, which is the approximate transit time of seeds through the gut of *Cebus* (see Wehncke *et al.* 2003). Locations in the area were determined by compass and pedometer. Tracking data were supplied by Janson & Di Bitetti which corresponded to a project that was run during 1998. Descriptive statistic was presented according to mean ± SE.

IDENTIFYING LONG-DISTANCE SEED DISPERSAL EVENTS

To identify long-distance seed dispersal events we compared the expected seed rain (seed density) with an estimation of the actual distribution of seeds within a plot of 265,000 m^2. The study area was divided into squares of 5 × 5 m totalling 10,600 squares. To estimate the expected *Miconia* seed density for each square, we developed a simulation model using the positions of all the *Miconia* trees within the plot and an equation describing seed density as a function of the distance from the parent tree (see results "seed shadows from isolated trees"). Reproductive *Miconia* trees were censused along seven transects 20 m wide and varying from 100 to 600 m long, thus totalling an area of 44,400 m^2. An exhaustive survey of all the *Miconia* trees were restricted to the area of transects. This area was selected because we have information on the distribution of reproductive *Miconia* trees and on the number of *Miconia* seeds captured in traps. The observed *Miconia* seed rain per square was calculated using data from 61 seed traps that measured the annual *Miconia* fruit production (from July 97 to August 98) reported by Di Bitetti (2001). As a visual method to show differences in densities estimated by both methods we used the Distance-Weighted Least Squares Fitting within STATISTICA (1984-2000 StatSoft, Inc).

To evaluate the existence and frequency of long-distance seed dispersal events, we focused on the 5 × 5 m squares containing seed traps. We compared the number of seeds observed with the number expected using the Mann-Withney test. In particular, to identify long-distance seed dispersal events, we selected those traps for which the number of seeds observed was much greater than that expected, and checked whether *Miconia* trees were present or absent in a 30 m radius from the trap.

Results

CONSEQUENCES OF SEED DISPERSAL BY *CEBUS* FOR *MICONIA* SEEDS

The model accounting for the effects of seed passage through the monkeys gut and of dispersal distance on seedling emergence, indicated that both distance and the interaction term (distance × treatment) had a significant effect ($\chi^2_{3,1076} = 6.4$, $P = 0.0002$). Seeds planted 50 m away from the parent trees had a higher probability (0.017 ± 0.033) of emergence than those below the crown (0.009 ± 0.015) ($\chi^2_{1,1079} = 7.7$, $P = 0.005$). As indicated by the significance of the interaction term ($\chi^2_{1,1079} = 4.1$, $P = 0.04$), defecated and control seeds only differed in emergence at 50 m from the crowns (Fig. 1). Although control seeds germinated more than defecated seeds, at those distances only defecated seeds are commonly found. Therefore, the effect of moving seeds away from parent trees has clear positive consequences on seed germination and seedling survival for *Miconia* (Fig. 1). There was not a significant effect of treatment (transit through the gut) on seedling emergence ($\chi^2_{1,1079} = 1.5$, $P = 0.22$).

SEED SHADOWS OF ISOLATED *MICONIA* TREES

The total seed rain inputs below the crown were 254,000 seeds m^{-2}, and 1,100 seeds m^{-2} at 20 m away from crowns. The majority of seeds captured corresponded to fallen ripe fruits (193,700 seeds m^{-2}). Individually dispersed seeds accounted for (8%) of seed rain.

Based on the censuses carried out in 1998, we described the seed shadow of isolated *Miconia* trees ($R^2 = 0.71$; all parameter estimates were significant $P < 0.0001$), (Fig. 2). The shape of the seed shadow of focal *Miconia* trees is represented by the equation $\ln y = b (\ln x) + a$, (where y = number of seeds/m^2, x = distance from the focal tree in meters, b = -1.96, and a = 8.74). We estimated the number of seeds fallen per m^2 below crown, and those at 5, 10 and 20 m from crowns. A great reduction in seed density was evidenced at distances farther than 5 meters from the focal tree (Fig. 2). According to the model, we should find 18 seeds/m^2 at 20 m, 3 seeds/m^2 at 50 m, and 1 seed/m^2 at 100 m.

FEEDING PATTERNS OF *CEBUS* AND ITS EFFECT AS SEED DISPERSER OF *MICONIA*

Miconia was the most heavily consumed fruit by *Cebus* during the period of study (82% of feeding events corresponded to *Miconia*, $n = 142$), and seeds of this species were also abundant in the faecal samples collected (mean number of seeds per faecal sample = 136 ± 155, $n = 26$). If we consider our estimation that one *Cebus* individual produces 8-10 defecations per day, it would disperse an estimated number of 1,088 *Miconia* seeds per day, and our focal group of 30 individuals, would disperse > 32,500 seeds of *Miconia* per day. During the study period the group spent 38.4 ± 27 min per *Miconia* fruiting tree (range: 4 to 134 min). *Cebus* travelled an average of 3,068 ± 430 m per day ($n = 30$, corresponding to 357 h of observations). They move swallowed *Miconia* seeds from 50 to 1150 m away from parent plants, with the highest probability of seed dispersal ranging between 300 to 400 m, and a mean distance of seed travel of 382 (± 227) m ($n = 76$). When we compared the natural seed shadow of *Miconia* with the seed shadow generated by *Cebus* dispersal, we found a clear effect of monkeys because they move seeds hundreds of meters away from the parent trees (Fig. 3).

MICONIA SEED SHADOW DERIVED FROM THE SIMULATION MODEL: IDENTIFYING LONG-DISTANCE SEED DISPERSAL EVENTS

The expected distribution of *Miconia* seeds is shown in Fig. 4a., and the observed distribution in Fig. 4b. The comparison between the expected and observed matrixes of seed densities coincided in one large area (see the bottom-right-hand corner of the plot, Figs. 4a and b) where the majority of *Miconia* trees were grouped. However, the matrix of observed seed densities showed another area of high concentration of *Miconia* seeds (see the top-left corner, Fig. 4b), that matched very well with an area reported to have been used very frequently by the group of monkeys under study (Di Bitetti 2001). Focusing only in those squares containing seed traps, we found significant differences between the expected and the observed number of seeds per square ($U = 2.48$, $P = 0.013$, $n = 61$). We found that four out of 61 traps had no *Miconia* trees in a 30 m radius. These four traps contained 627 seeds, which represented 1% of the total number of seeds in all traps. Coincidentally, between September and October 1998 the monkey focal group had been feeding on bananas on a daily basis at feeding stations (Di Bitetti 2001). These areas that were used more intensively by *Cebus* and coincided with the areas occupied by the four traps, resulted in higher than expected dispersal of *Miconia* around these sites (Fig. 4b). These cases represented clear events of long-distance seed dispersal. In addition, these events moved seeds far from any other conspecific reproductive tree.

Discussion

CONSEQUENCES OF *CEBUS* DISPERSAL FOR *MICONIA* SEEDS

Dispersal by monkeys reduced mortality of seeds and seedlings by placing seeds away from conspecific trees. We found a significantly strong effect of distance on seed germination and establishment. Nevertheless, *Miconia* seeds seemed to be negatively affected by the transit through the gut of monkeys, since control seeds germinated in higher proportions than defecated seeds at distances far from conspecifics. Fungi have been suggested as mortality agents and as a possible explanation of the rare pattern observed here. Evidence is accumulating that fungal pathogens may regulate the distribution and abundance of plant populations in tropical forests, which supports this result (Augspurger 1983, 1984, Martínez-Ramos & Alvarez-Buylla 1986, Garwood 1989, Gilbert *et al.* 1994). In a similar study, Dalling *et al.* (1998) found that treatment of seeds with a fungicide reduced mortality up to 47% in *Miconia*, and that differences in mortality of *Miconia* seeds were largely attributable to location effects (comparison of below-crown sites vs. sites 30 m away). However, the extent to which seed-infecting fungi are specific to their hosts is still unknown. Crist & Friese (1993) provide evidence that fungi play an important role in soil seed dynamics, but they also suggest that nonlethal seed-infecting fungi might also reduce the attractiveness of seeds to granivorous ants. In any case, in our experiment, at 50 m away from parent plants, animal-dispersed seeds are the ones most likely to be found. Based on the frequently tested Janzen-Connell model (Clark & Clark 1984, Harms *et al.* 2000) and according to studies that argue that long-distance endozoochorous seed dispersal leads to higher survival rates than those dispersed in the vicinity of the parent plant, *Cebus* conferred an important advantage placing seeds at long distances from parent plant.

NATURAL AND *CEBUS* DISPERSED SEED SHADOWS

Evidence here and elsewhere (Alvarez-Buylla & Martínez-Ramos 1990, Dalling *et al.* 1997, 1998, Fleming & Heithaus 1981) shows that for many pioneer species seed densities decline leptokurtically with distance from the parent plant, with an extended tail of long-distance dispersal. Here we found a similar pattern with a pronounced decline in seed densities away from *Miconia* crown. However, it is more informative to link this pattern with the pattern of seed dispersal produced by animals. This helps to understand the real shape of seed shadow and range of dispersal. In this study we showed that *Cebus* monkeys play an important role in the dispersal of *M. pusilliflora* seeds in Iguazú. During the study period *M. pusilliflora* was almost the only species of fruit consumed by *Cebus* monkeys, although *Miconia* was also visited by birds and possibly by rodents. Fruits of *Miconia* were heavily consumed by *Cebus* and seeds were left in viable conditions. One of the most important characteristics of *Cebus* feeding and dispersal patterns was the distance at which *Miconia* seeds were dispersed. When we focus our attention on the tail end of *Miconia* seed shadow we found that *Cebus* provided seeds the opportunity to escape the neighbourhood of the parent plant, and in turn allowed seeds to colonize new and potentially favourable microsites for seedling establishment. Additionally, the time they spent on each tree coupled with the transit time of seeds through the gut of monkeys showed that *Cebus* spent on average much less time per tree than that necessary for seeds to be defecated. This greatly increases the likelihood that seeds are dispersed away from *Miconia* crowns.

MICONIA SEED SHADOW DERIVED FROM THE SIMULATION MODEL: IDENTIFYING LONG-DISTANCE SEED DISPERSAL EVENTS

Here we identified long-distance seed dispersal events, but also showed the frequency of these processes that surely have the most important biological consequences. The comparison between the expected and observed matrixes of seed densities showed an area of high concentration of *Miconia* seeds (see the top-left corner, Fig. 4b), that matched very well with an area reported to have been used very frequently by the group of monkeys under study (Di Bitetti 2001). Fortunately, food provisioning experiments that have been run during the same study period (Di Bitetti 2001) helped us to easily explain the fact that some traps had relatively higher numbers of *Miconia* seeds. When food was provided monkeys reduced the area used from 137 to 85 1-ha quadrats which were used still more intensively (Di Bitetti 2001). This experiment explained the occurrence of traps containing *Miconia* seeds with no tree around or at least at distances < 30 meters from it.

These cases represent clear events of dispersal far from any conspecific reproductive tree. If we consider that those seeds have the greater chance of survival, the 1% reported here represented the annual rate of *Miconia* long-distance seed dispersal produced by only one group of *Cebus,* which probably have the highest biological consequences such as the genetic homogenization of plant populations. Long-distance seed dispersal has been commonly considered as occurring through rare, infrequent events (Clark *et al.* 1999, Higgins & Richardson 1999, Bullock & Clarke 2000, Cain *et al.* 2000, but see Fragoso *et al.* 2003). However in this forest the yield of seed dispersers is not limited only to *Cebus* monkeys and some species are dispersed by wind. As other studies have indicated, long-distance seed dispersal by animals may be neither rare nor unpredictable once we understand the movement patterns of animals (Fragoso & Huffman 2000, Fragoso *et al.* 2003). Ideally, having a better picture of the rate of long-distance seed dispersal events produced by the entire yield of dispersers and for a sufficient number of plant species for a particular forest environment would help to determine whether hese events are more common than expected.

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Figure legends

Figure 1. Germination of control and defecated by *Cebus* seeds of *Miconia pusilliflora*, below the crown of parent trees and at 50 m away from the crown.

Figure 2. Curve fit of the linear model describing the seed shadow of isolated *Miconia* focal trees (seed density/m^2) at several distances (m) away from parent trees.

Figure 3. Seed shadows of isolated *Miconia* focal trees, and that generated by *Cebus*, at different distances (m) from the crown.

Figure 4. Estimations of: a) the expected number of *Miconia* seeds/m^2 and b) the observed number of *Miconia* seeds/m^2 by the distance weighted least squares graphic method. Each quadrate represents an area of 5 x 5 m in the field. Colours represent seed densities/m^2.

Figure 1

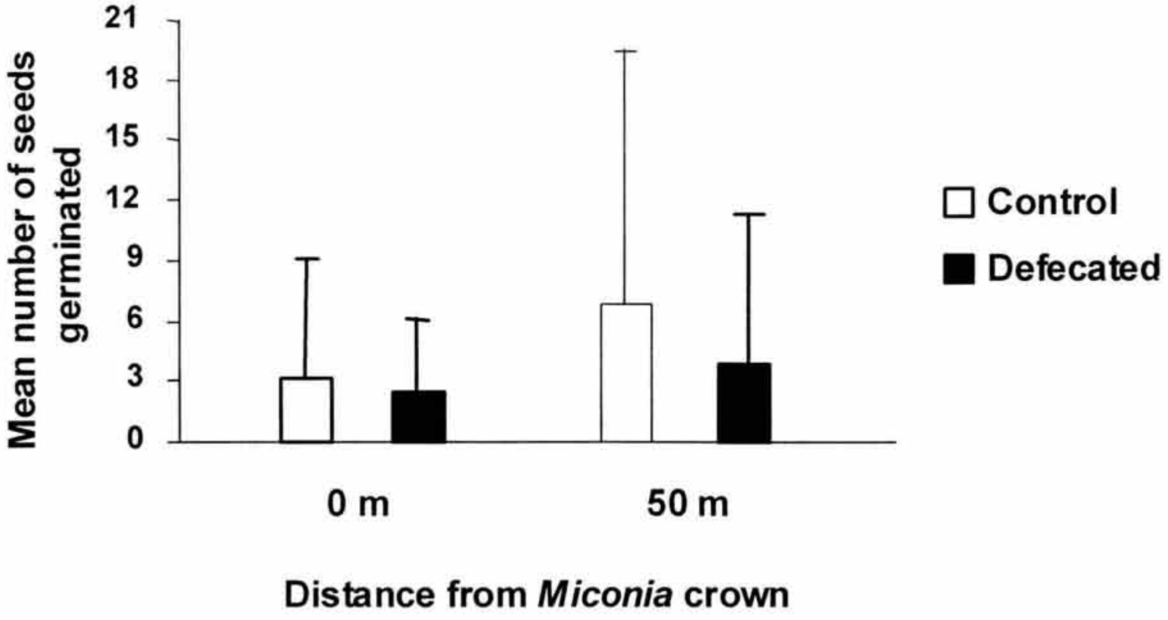

Mean number of seeds germinated
21
18
15
12
9
6
3
0
0 m
50 m
Distance from *Miconia* crown
☐ Control
■ Defecated

Figure 2

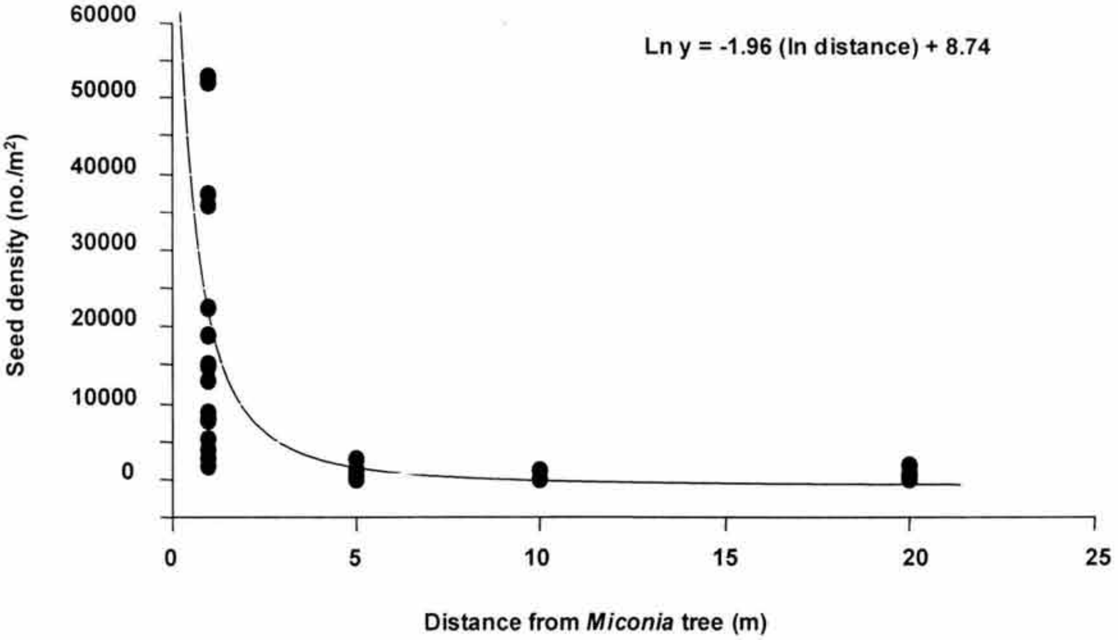

Ln y = -1.96 (ln distance) + 8.74
Seed density (no./m²)
60000
50000
40000
30000
20000
10000
0
0
5
10
15
20
25
Distance from *Miconia* tree (m)

Figure 3

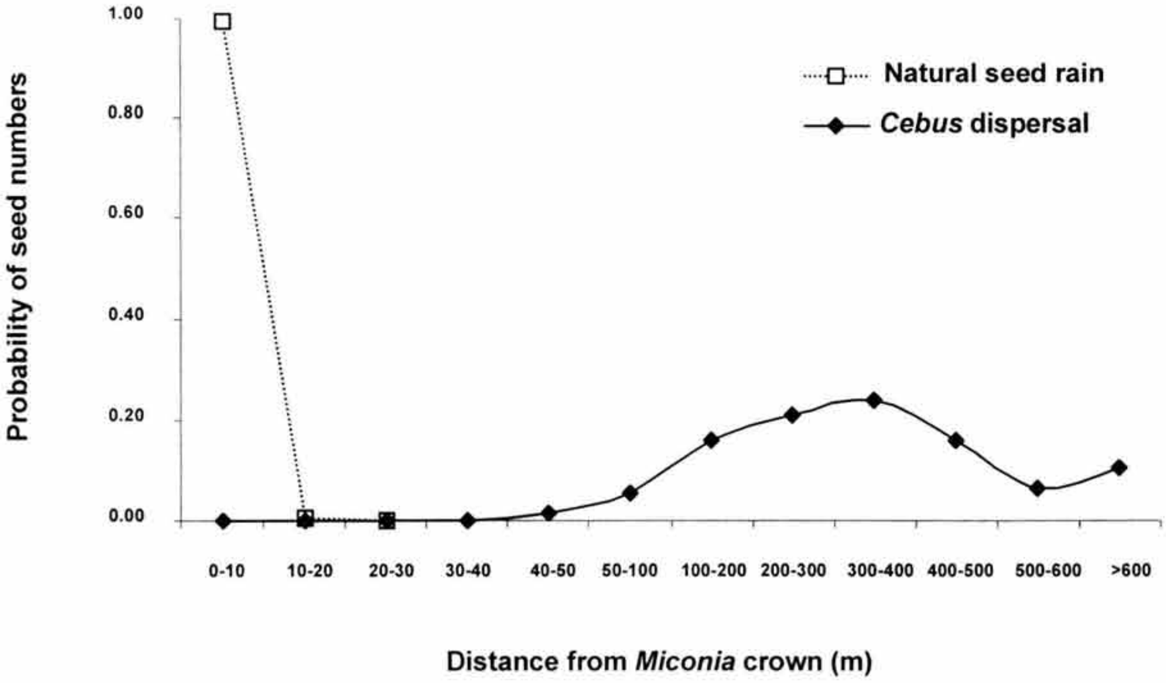

Probability of seed numbers
1.00
0.80
0.60
0.40
0.20
0.00
Natural seed rain
Cebus dispersal
0-10
10-20
20-30
30-40
40-50
50-100
100-200
200-300
300-400
400-500
500-600
>600
Distance from *Miconia* crown (m)

Figure 4a

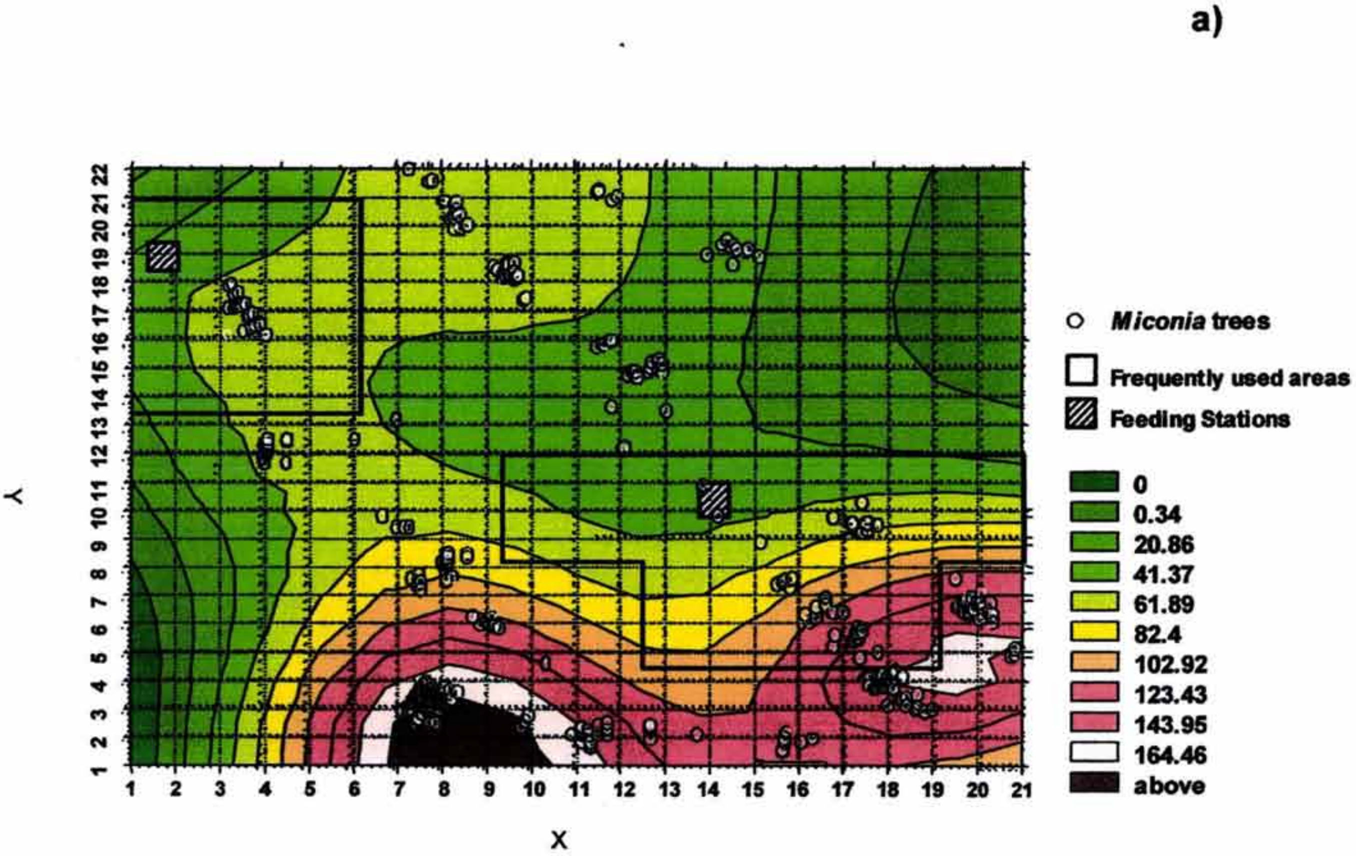
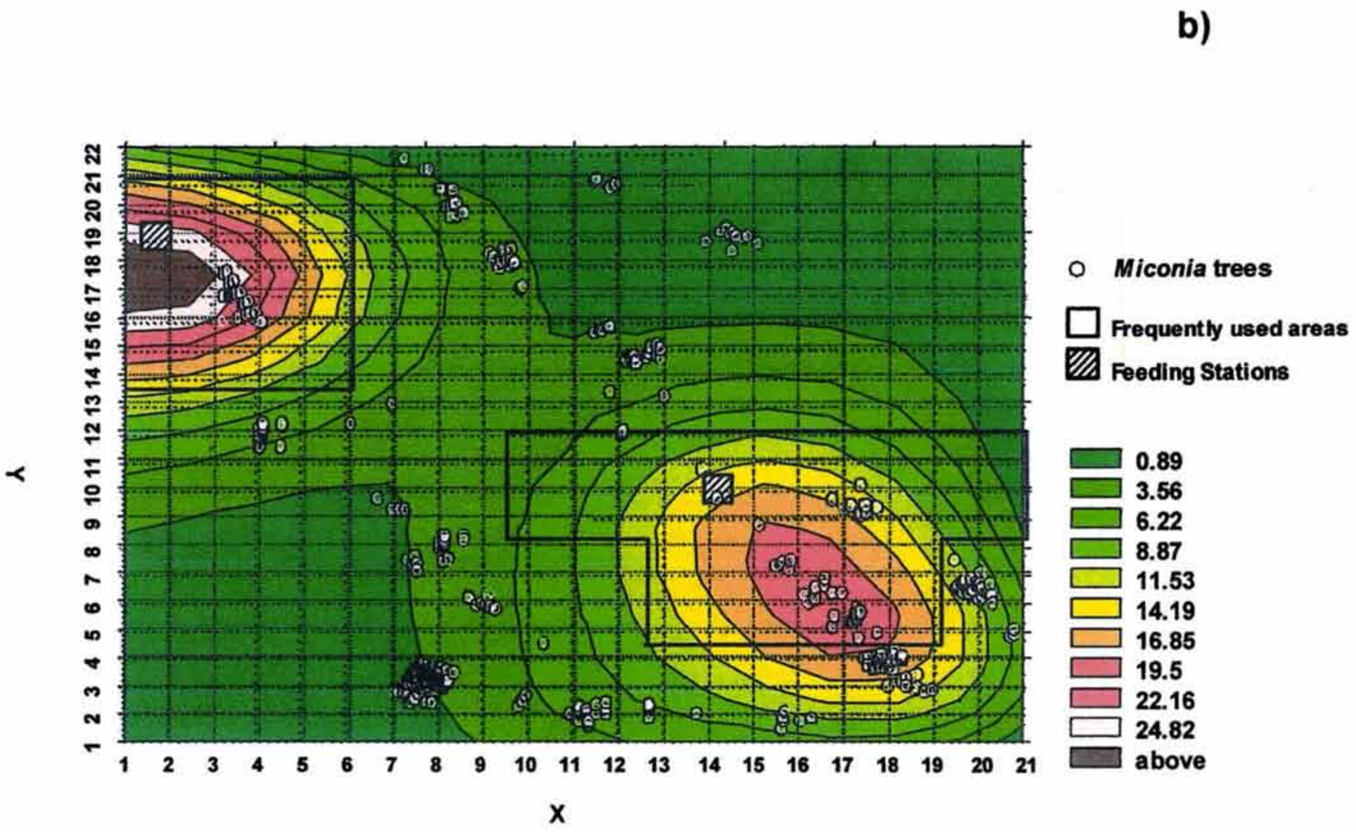

a)
Y
X
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
○ *Miconia* trees
☐ Frequently used areas
▨ Feeding Stations
0
0.34
20.86
41.37
61.89
82.4
102.92
123.43
143.95
164.46
above

Figure 4b


b)
Y
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
X
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
○ *Miconia* trees
☐ Frequently used areas
▨ Feeding Stations
0.89
3.56
6.22
8.87
11.53
14.19
16.85
19.5
22.16
24.82
above

DISCUSIÓN GENERAL

Diversos estudios postulan que las interacciones entre las plantas y los frugívoros "estrictos" y "no-estrictos" tienen diferentes consecuencias ecológicas y evolutivas para las especies interactuantes (Fig. 1, de la Introducción); (Janzen 1970, Snow 1971, McKey 1975, Howe y Estabrook 1977, Howe y Smallwood 1982). Esto surge de enunciados basados en que la dieta de los frugívoros estrictos está compuesta por un alto porcentaje de frutos, lo cual supone una dispersión efectiva de las semillas que consumen. Como consecuencia, se propone que muchos de los atributos de los frutos son el resultado de las presiones de selección ejercidas por estos animales (Fleming et al. 1987, 1993, Russo 2003); (Fig. 1, de la Introducción). Por otro lado, se piensa que los frugívoros no estrictos, al consumir una gran variedad de alimentos además de frutos, son menos constantes (frecuentes) en las visitas a los árboles de una especie particular y se ha sugerido que deben ejercer presiones de selección mucho más débiles sobre las especies que consumen (Fleming et al. 1993); (Fig. 1, de la Introducción). Sin embargo, las clasificaciones normalmente utilizadas para explicar el papel de los animales en la dispersión de las semillas, frugívoros especialistas como diseminadores de alta calidad y frugívoros generalistas como diseminadores de alta cantidad (McKey 1975, Howe & Estabrook 1977) podrían no ser las adecuadas. Según Schupp (1993), una elevada calidad de la dispersión podría compensar y hasta elevar la eficacia de un frugívoro como dispersor (Fig. 2, de la Introducción). Esta última situación es la que precisamente se observa en el caso de *Cebus* en los resultados de este estudio.

En este estudio encontramos que a lo largo de su gradiente de distribución, en tres tipos de bosques diferentes de América, *Cebus* se alimentó de lo que estuvo disponible confirmando su comportamiento generalista. Sin embargo, algunos patrones de frugivoría y movimiento de *Cebus* varían de acuerdo al gradiente de diversidad de frutos de los sitios y esto tiene consecuencias en el patrón de dispersión de las semillas. Esto fue más evidente en el ambiente menos diverso donde las distancias de dispersión resultantes fueron mas largas. La calidad de la dispersión provista por un animal no es constante, y puede depender del escenario ecológico particular donde el proceso de dispersión ocurra. Aunque no se puede determinar una relación causal entre diferentes contextos de diversidad, patrones de frugivoría y de dispersión por *Cebus*, podemos concluir que animales con una dieta generalista tienen el potencial de ejercer efectos importantes como dispersores de semillas influenciando procesos evolutivos y ecológicos en la dinámica de los bosques tropicales y subtropicales. Consecuencias de estos tipos de interacciones ejercidas sobre un gran número de especies de plantas caracterizadas por diferentes síndromes de dispersión, serían una explicación de los conflictos que se generan en las interacciones planta-animal para seleccionar caracteres óptimos de dispersión en respuesta a un determinado tipo de dispersor. Así, este tipo de interacciones tienen el potencial de desacoplar relaciones estrechas y relajar presiones de selección ejercidas por frugívoros estrictos sobre los atributos de las plantas que consumen, lo cual finalmente es lo que comúnmente se observa en la naturaleza. Por otro lado, la variación en los ensambles de dispersores a escalas regionales, tanto en la identidad de los dispersores que forman el ensamble, como en la respuesta de éstos a los diferentes atributos en las plantas, es otro factor importante que contribuye a esta inconsistencia (Wheelwright y Orians 1982, Howe 1984, Herrera 1985).

En particular el patrón de defecación producido por *Cebus* juega un papel muy importante en el destino de las semillas, ya sea por un efecto individual o en conjunto: (i) de un incremento en la supervivencia a corto plazo una vez que las semillas son depositadas, debido a la baja remoción de las mismas, (ii) porque éstas son depositadas lejos de los árboles parentales, (iii) porque los sitios donde finalmente caen, lejos de plantas conespecíficas, pueden en general ser considerados "sitios seguros", y (iv) porque algunos de estos eventos de dispersión suelen ser a larga distancia. Si consideramos que estas semillas dispersadas a largas distancias son las que tienen mayores probabilidades de sobrevivencia, el efecto de *Cebus* no sólo es importante para la estructura genética de las poblaciones de plantas, en las tasas de migración y/o invasión de plantas, sino también en el contexto de la fragmentación del hábitat. Así, este efecto está asociado al componente de calidad de la dispersión y lo que es importante es que tiene el potencial de diluir cualquier efecto del componente de cantidad de remoción y dispersión de semillas producido por cualquier agente dispersor (Zhang y Wang 1995, Wehncke *et al.* 2004).

Por lo tanto, los frugívoros "no estrictos" pueden también realizar una dispersión efectiva de las semillas que consumen. Esto ocurre porque a pesar de remover pocas semillas de una especie particular, cada una de ellas tiene una alta probabilidad de establecimiento. Por otro lado, las semillas removidas son depositadas de manera no concentrada y en sitios alejados de los árboles parentales y de otras plantas conespecíficas.

En el contexto de la hipótesis de la limitación de la dispersión (Hurtt y Pacala 1995), el patrón de dispersión de semillas por parte de *Cebus* puede tener implicaciones importantes en el mantenimiento de la diversidad de los bosques. Recientemente, diversos estudios hicieron hincapié en el papel que juega la limitación de la dispersión en la diversidad de los bosques tropicales (Dalling et al. 1998, Svenning 2001). En este escenario las semillas de las especies competitivamente dominantes no llegan a los sitios disponibles para establecerse, permitiendo de este modo el establecimiento y persistencia de las especies competitivamente inferiores. Por lo tanto, la dominancia por parte de unas pocas especies es reducida y la diversidad se incrementa. En este sentido, el patrón de dispersión heterogéneo de *Cebus*, puede tener consecuencias positivas tanto al nivel de la población como al de la comunidad.

En los últimos años diversos estudios acerca de la dispersión a larga distancia han resaltado la importancia crítica que estos eventos tienen en el contexto de la fragmentación del hábitat (Malanson y Armstrong 1996), las tasas de migración y las invasiones de plantas (Shaw 1995, Higgins y Richardson 1999, Richardson *et al.* 2000), y en la diferenciación genética de la poblaciones (Le Corre *et al.* 1977). Sin embargo son poco comunes los trabajos que aborden el estudio de la dispersión a larga distancia (Cain *et al.* 2000, Fragoso *et al.* 2003). En este estudio mostramos que *Cebus* tiene el potencial de dispersar las semillas a largas distancias y lejos de árboles conespecíficos. Estos eventos pueden tener consecuencias biológicas importantes, ya que pueden contribuir a la homogeneización genética de algunas poblaciones de plantas. Al mismo tiempo, es evidente que la fragmentación del hábitat incide negativamente, interrumpiendo estos procesos. Como la mayoría de estos eventos a larga distancia ocurren dentro de ambientes naturales complejos y estos ambientes con el tiempo están siendo cada vez mas fragmentados, la capacidad de las semillas para moverse a largas distancias también se ve más reducida, aunque algunas de ellas logren saltar entre fragmentos.

Por último, el creciente número de estudios de dispersión de semillas por primates ha mostrado que éstos juegan un papel fundamental en los ecosistemas donde habitan. Sin embargo, cada nuevo hallazgo ilustra la complejidad de estos sistemas debido a los diferentes procesos que están involucrados, y esto es lo que ha dado surgimiento a una variedad de nuevas avenidas de investigación. Los primates no sólo constituyen una proporción importante de la biomasa de frugívoros en los bosques tropicales y subtropicales, sino que, a través de sus interacciones con las plantas y otros animales, tienen un papel fundamental en el funcionamiento de los ecosistemas.

Encontramos que *Cebus* tiene un importante papel en la dispersión de semillas de muchas especies de plantas principalmente debido a que: (i) a pesar de tener una dieta generalista, consume una alta diversidad de frutos, (ii) ejerce un tratamiento suave a las semillas, tanto antes como después de ser ingeridas y presenta tiempos relativamente cortos de pasaje de semillas por el tracto digestivo, (iii) permanece poco tiempo en los árboles de los que se alimenta, depositando las semillas lejos de los árboles parentales, (iv) en general, dispersa las semillas a largas distancias, (v) presenta un patrón de defecación heterogéneo, depositando las semillas "en tránsito" a lo largo de sus rutas de movimiento y con poca cantidad de material fecal, y (vi) lo cual como consecuencia, reduce la remoción post-dispersión de estas semillas ya sea por dispersores secundarios y/o depredadores.

A pesar de lo complejo de los estudios, es necesario conocer la calidad de la dispersión de semillas en términos de su efecto sobre la sobrevivencia de semillas per cápita y el establecimiento de las plántulas. Es imprescindible incluir los efectos derivados de los dispersores "no estrictos" ya que éstos constituyen una gran diversidad en la gama de estrategias de dieta existentes. También es importante considerar los efectos en conjunto de las especies dispersoras una vez que se encuentran formando parte de ensambles compuestos por diferentes especies. Debido a que estos efectos pueden variar en espacio y tiempo, sería interesante considerar el proceso de la dispersión explorando diversas escalas para conocer a qué escala espacial ocurren los patrones funcionales más significantes del proceso de la dispersión, como también conocer si este escalamiento es consistente o no entre unidades geográficas grandes.

Hasta ahora no ha sido fácil describir qué ocurre en la cola de las distribuciones de la sombra de semillas producida por la dispersión a larga distancia. Por lo tanto, es en estos eventos a larga distancia en los cuales debería enfocarse la mayor atención. Finalmente, con el fin de mantener la capacidad de regeneración de los remanentes de bosque, sería interesante identificar los ensambles de especies, tanto de animales como de plantas, que deberían ser el foco de los esfuerzos de conservación.

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" E yendo por el dicho río de Iguazú abajo era la corriente de él tan grande, que corrían las canoas por él con mucha furia; y esto causólo que muy cerca de donde se embarcó da el río un salto por unas peñas abajo muy altas, y da el agua en lo bajo de la tierra tan grande golpe, que de muy lejos se oye; y la espuma del agua, como cae con tanta fuerza, sube en alto dos lanzas y más,..."

De cómo el Gobernador caminó con canoas por el río de Iguazú, y por salvar un mal paso de un salto que el río hacía, llevó por tierra las canoas una legua a fuerza de brazos.
CAPÍTULO XI, COMENTARIOS DE ÁLVAR NÚÑEZ CABEZA DE VACA, Adelantado y Gobernador del Río de la Plata, (1555).