

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

E. V. WEHNCKE*, S. P. HUBBELL†‡, R. B. FOSTER§ and J. W. DALLING†¶

Departamento de Ecología Evolutiva, Universidad Nacional Autónoma de México, Apartado 70–275, México DF 04510, México, †Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama, ‡Department of Botany, University of Georgia, Athens, GA 30602, USA, §Department of Botany, The Field Museum, Chicago IL 60605, USA, and ¶Department of Plant Biology, University of Illinois, Champaign-Urbana, IL 61801, USA

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.

Journal of Ecology (2003) **91**, 677–685

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

*Correspondence: Elisabet Wehncke, Laboratorio de Interacciones Planta-Animal, Departamento de Ecología Evolutiva, Apartado 70–275, Ciudad Universitaria, Circuito Exterior, 04510 México DF, México (fax +52 5 56161976, e-mail elisabetw@ecologia.unam.mx).

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 understory 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 ($9^{\circ}10' N$, $79^{\circ}51' W$). The island extends over 15.6 km² 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 , $n = 26$;

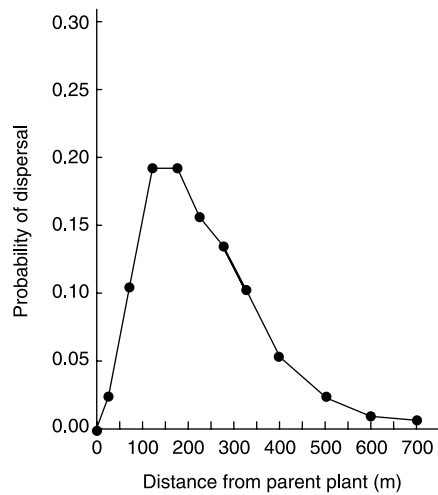


Fig. 1 Probability of seed dispersal by *Cebus* away from a parent plant. Estimates are based on individuals inside and outside the 50-ha plot.

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.

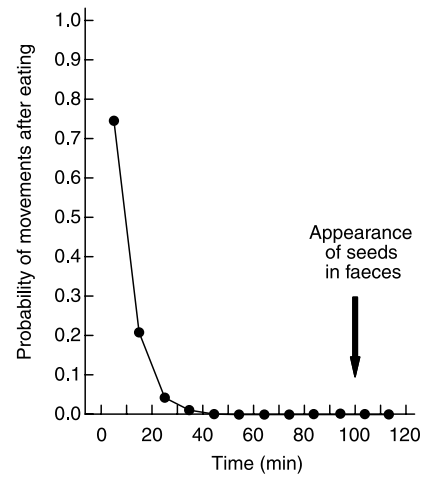


Fig. 2 Probability of movement of *Cebus* away from fruiting trees after starting feeding.

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

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

tion 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.

Acknowledgements

This research was funded by the Smithsonian Tropical Research Institute (STRI) through a Short-Term Fellowship to E.W. We especially thank Osvaldo Calderón for identification of the plant and seed samples. We thank STRI for logistic support, Joseph Wright and Rolando Perez for access to unpublished data, and Juan José Rodríguez and Javier Ballesteros for help in the field. Hugh Drummond, César Domínguez, Gerardo Ceballos, Sabrina Russo, Helene Muller-Landau and Carol Augspurger provided helpful comments on the manuscript.

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.

References

- Augsburger, C.K. (1983) Seed dispersal of the tropical tree *Platypodium elegans* and the escape of its seedlings from fungal pathogens. *Journal of Ecology*, **71**, 759–772.
- Augsburger, C.K. (1984) Seedling survival of tropical tree species: interactions of dispersal distance, light gaps and pathogens. *Ecology*, **65**, 1705–1712.
- Barone, J.A. (1996) *Herbivory and tropical tree diversity: a test of the Janzen–Connell Model*. PhD Thesis, University of Utah.
- Bleher, B. & Bohning-Gaese, K. (2001) Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia*, **129**, 385–394.
- Burdon, J.J. & Chilvers, G.A. (1982) Host density as a factor in plant disease ecology. *Annual Review of Phytopathology*, **20**, 143–166.
- Chapman, C.A. (1989) Primate seed dispersal: the fate of dispersed seeds. *Biotropica*, **21**, 148–154.
- Chapman, C.A. (1995) Primate seed dispersal: coevolution and conservation implications. *Evolutionary Anthropology*, **4**, 73–110.
- Clark, D.A. & Clark, D.B. (1984) Spacing dynamic of a tropical rain forest tree: evaluation of the Janzen–Connell model. *American Naturalist*, **124**, 769–788.
- Clark, J.S., Silman, M., Kern, R., Macklin, E. & Hill Ris Lambers, J. (1999) Seed dispersal near and far: patterns across temperate and tropical forests. *Ecology*, **80**, 1475–1494.
- Coley, P.D. & Barone, J.A. (1996) Herbivory and plant defenses in tropical forests. *Annual Review of Ecology and Systematics*, **27**, 305–335.
- Condit, R., Hubbell, S.P. & Foster, R.B. (1992) Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *American Naturalist*, **140**, 261–286.
- Condit, R. (1998) *Tropical Forest Census Plots: Methods and Results from BCI, Panamá, and Comparisons with Other Plots*. Springer-Verlag, Berlin.
- Crawley, M.J. (1990) The population dynamics of plants. *Philosophical Transactions of the Royal Society of London*, **B330**, 125–140.
- Croat, T.B. (1978) *Flora of Barro Colorado Island*. Stanford University Press, Stanford, CA.
- Dalling, J.W. & Hubbell, S.P. (2002) Seed size, growth rate and gap microsite conditions as determinants of recruitment success for pioneer species. *Journal of Ecology*, **90**, 557–568.
- Dalling, J.W., Muller-Landau, H.C., Wright, S.J. & Hubbell, S.P. (2002) Role of Dispersal in the recruitment limitation of neotropical pioneer species. *Journal of Ecology*, **90**, 714–727.
- Dalling, J.W., Swaine, M.D. & Garwood, N.C. (1998) Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology*, **79**, 564–578.
- Denslow, J.S., Moermond, T.C. & Levey, D.J. (1986) Spatial components of fruit display in understory trees and shrubs. *Frugivores and Seed Dispersal* (eds A. Estrada & T.H. Fleming), pp. 37–44. Dr W. Junk Publishers, Dordrecht.
- Estrada, A. & Coates-Estrada, R. (1984) Fruit eating and seed dispersal by howling monkeys (*Alouatta palliata*) in the tropical rain forest of Los Tuxtlas, Mexico. *American Journal of Primatology*, **6**, 77–91.
- Forget, P.M. (1993) Post-dispersal predation and scatterhoarding of *Dipteryx panamensis* (Papilionaceae) seeds by rodents in Panamá. *Oecologia*, **94**, 255–261.
- Foster, R.B. (1982) The seasonal rhythm of fruitfall on Barro Colorado Island. *The Ecology of a Tropical Forest* (eds A. Rand & E. Leigh), pp. 151–172. Smithsonian Institution Press, Washington, DC.
- Foster, R.B. & Brokaw, N.V.L. (1982) Structure and history of the vegetation of Barro Colorado Island. *The Ecology of a Tropical Forest* (eds A. Rand & E. Leigh), pp. 67–81. Smithsonian Institution Press, Washington, DC.
- Fragoso, J.M.V. (1997) Tapir-generated seed shadows: scale-dependent patchiness in the Amazon rain forest. *Journal of Ecology*, **85**, 519–529.
- Garber, P.A. (1986) The ecology of seed dispersal in two species of Callitrichid Primates (*Saguinus mystax* and *Saguinus fuscicollis*). *American Journal of Primatology*, **10**, 155–170.
- Gautier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J.P., Dubost, G., Emmons, L., Erard, C., Heckestweiler, P., Mounqazi, A., Roussillon, C. & Thiollay, J.M. (1985) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia*, **65**, 324–337.
- Gilbert, G.S. & De Steven, D. (1996) A canker disease of seedlings and saplings of *Tetragastris panamensis* (Burseraceae) caused by *Botryosphaeria dothidea* in a lowland tropical forest. *Plant Disease*, **80**, 684–687.
- Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. (2001) Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology*, **89**, 47–959.
- Harms, K.E., Wright, S.J., Calderon, O., Hernandez, A. & Herre, E.A. (2000) Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature*, **404**, 493–495.
- Hladik, A. & Hladik, C.M. (1969) Rapports trophiques entre végétation et primates dans la forêt de Barro Colorado (Panamá). *Revue d'Ecologie: La Terre et la Vie*, **23**, 25–117.
- Holbrook, K.M. & Smith, T.B. (2000) Seed dispersal and movement patterns in two species of *Ceratogymna* hornbills in a West African tropical lowland forest. *Oecologia*, **125**, 249–257.
- Howe, H.F. (1977) Bird activity and seed dispersal of a tropical wet forest tree. *Ecology*, **58**, 539–550.
- Howe, H.F. (1989) Scatter and clump dispersal and seedling demography: hypothesis and implications. *Oecologia*, **79**, 417–426.
- Howe, H.F. & Primack, R.B. (1975) Differential seed dispersal by birds of the tree *Casearia nitida* (Flacourtiaceae). *Biotropica*, **7**, 278–283.
- Howe, H.F. & Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, **13**, 201–228.
- Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & Loo de Lao, S. (1999) Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science*, **283**, 554–557.
- Hurt, G.C. & Pacala, S.W. (1995) The consequences of recruitment limitation: reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, **176**, 1–12.
- Janson, C.H. (1983) Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science*, **219**, 187–189.
- Janson, C.H. (1985) Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). *Behavioural Ecology Sociobiology*, **18**, 125–138.
- Janson, C.H. (1990a) Social correlates of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, **40**, 910–921.
- Janson, C.H. (1990b) Ecological consequences of individual spatial choice in foraging groups of brown capuchin monkeys, *Cebus apella*. *Animal Behaviour*, **40**, 922–934.

- Janson, C.H., Stiles, E.W. & White, D.W. (1986) Selection on plant fruiting traits by brown capuchin monkeys: a multivariate approach. *Frugivores and Seed Dispersal* (eds A. Estrada & T. H. Fleming), pp. 83–92. Dr W. Junk Publishers, Dordrecht.
- Janzen, D.H. (1971) The fate of *Scheelea rostrata* fruits beneath the parent tree: predispersal attack by bruchids. *Principes*, **15**, 89–101.
- Janzen, D.H., Miller, G.A., Hackforth-Jones, J., Pond, C.M., Hooper, K. & Janos, D.P. (1976) Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). *Ecology*, **57**, 1068–1075.
- Julliot, C. (1986) Seed dispersal by red howling monkeys (*Alouatta seniculus*) in the tropical rain forest of French Guiana. *International Journal of Primatology*, **17**, 239–258.
- Levey, D.J. (1987) Seed size and fruit-handling techniques of avian frugivores. *American Naturalist*, **129**, 471–485.
- Lieberman, D., Hall, I.B., Swaine, M.D. & Lieberman, M. (1979) Seed dispersal by baboons in the Shai Hills, Ghana. *Ecology*, **60**, 65–75.
- Lieberman, M. & Lieberman, D. (1986) An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. *Journal of Tropical Ecology*, **2**, 113–126.
- McKey, D. (1975) The ecology of coevolved seed dispersal systems. *Coevolution of Animals and Plants* (eds L.E. Gilbert & P.H. Raven), pp. 159–191. University of Texas Press, Austin, London.
- Milton, K. (1984) The role of food-processing factors in primate food choice. *Adaptations of Foraging in Nonhuman Primates* (eds P.S. Rodman & J.G.H. Cant), pp. 249–279. Columbia University Press, New York, USA.
- Mitchell, B.J. (1989) *Resources, group behavior, and infant development in white-faced capuchin monkeys*, *Cebus capucinus*. PhD Thesis, University of California, Berkeley.
- Mohr, C.O. (1947) Table of equivalent populations of North American mammals. *American Midland Naturalist*, **37**, 223–249.
- Muller-Landau, H.C., Wright, S.J., Calderon, O., Hubbell, S.P. & Foster, R.B. (2002) Assessing Recruitment Limitation: Concepts, Methods and Case-Studies from a Tropical Forest. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (eds D.J. Levey, W.R. Silva and M. Galetti), pp. 35–53. CABI Publishing, Wallingford, UK.
- Murray, K.G. (1988) Avian seed dispersal of three neotropical gap-dependent plants. *Ecological Monographs*, **58**, 271–298.
- Nathan, R. & Muller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278–285.
- Oppenheimer, J.R. (1968) *Behavior and ecology of the white-faced monkey, Cebus capucinus, on Barro Colorado Island*. PhD Thesis, University of Illinois, Urbana.
- Pacala, S.W. & Levin, S.A. (1997) Biologically generated spatial pattern and the coexistence of competing species. *Spatial Ecology: the Role of Space in Population Dynamics and Interspecific Interactions* (eds D. Tilman & P. Kareiva), pp. 204–232. Princeton University Press, Princeton, New Jersey, USA.
- Packer, A. & Clay, K. (2000) Soil pathogens and spatial patterns of seedling mortality in a temperate tree. *Nature*, **404**, 278–281.
- Ramírez, N. & Arroyo, M.K. (1987) Variación espacial y temporal en la depredación de semillas de *Copaifera pubiflora* Benth. (Leguminosae: Caesalpinioideae) en Venezuela. *Biotropica*, **19**, 32–39.
- Ribbens, E., Silander, J.A. & Pacala, S.W. (1994) Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology*, **75**, 1794–1806.
- Schupp, E.W. (1993) Quantity, quality, and the effectiveness of seed dispersal by animals. *Frugivores and Seed Dispersal* (eds A. Estrada & T.H. Fleming), pp. 15–29. Dr W. Junk Publishers, Dordrecht.
- Schupp, E.W. (2002) The efficacy of the dispersal agent. *Ecología y Conservación de Bosques Neotropicales* (eds M.R. Guariguata & G.H. Kattan), pp. 357–360. Libro Universitario Regional, Costa Rica.
- Schupp, E.W., Milleron, T. & Russo, S.E. (2002) Dispersal limitation and the origin and maintenance of species-rich tropical forests. *Seed Dispersal and Frugivory: Ecology, Evolution, and Conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 19–34. CABI Publishing, New York.
- Seaman, D.E. & Powell, R.A. (1996) An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology*, **77**, 2075–2085.
- Silman, M.R. (1996) *Regeneration from seed in a neotropical rain forest*. PhD Thesis, Duke University, Raleigh, North Carolina.
- Silverman, B.W. (1986) *Density Estimation for Statistics and Data Analysis*. Chapman & Hall, London, UK.
- Thies, W. (1998) *Resource and habitat use in two frugivorous bat species (Phyllostomidae: Carollia perspicillata and C. Castanea) in Panamá: mechanisms of coexistence*. PhD Thesis, University of Tübingen, Germany.
- Tilman, D. (1994) Competition and biodiversity in spatially structured habitats. *Ecology*, **75**, 2–16.
- Turnbull, L.A., Crawley, M.J. & Rees, M. (2000) Are plant populations seed-limited? A review of seed sowing experiments. *Oikos*, **88**, 225–238.
- Tutin, C.E.G., Williamson, E.A., Rogers, M.E. & Fernandez, M. (1991) A case study of a plant-animal relationship: *Colia lizae* and lowland gorillas in the Lopé Reserve, Gabon. *Journal of Tropical Ecology*, **7**, 181–199.
- Van der Pijl, L. (1969) Evolutionary action of tropical animals on the reproduction of plants. *Biology Journal of the Linnean Society*, **1**, 85–96.
- Webb, C.O. & Peart, D.R. (2000) Habitat associations of trees and seedlings in a Bornean rain forest. *Journal of Ecology*, **88**, 464–478.
- Webb, C.O. & Peart, D.R. (2001) High seed dispersal rates in faunally intact tropical rain forest: theoretical and conservation implications. *Ecology Letters*, **4**, 491–499.
- Wheelwright, N.T. & Orians, G.H. (1982) Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist*, **119**, 402–413.
- Windsor, D.M. (1990) Climate and moisture variability in a tropical forest: long-term records from Barro Colorado Island, Panamá. *Smithsonian Contributions to the Earth Sciences*, **29**, 1–145.
- Wolfheim, J.H. (1983) *Primates of the World: Distribution, Abundance, and Conservation*. University of Washington Press, Seattle.
- Worton, B.J. (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology*, **70**, 164–168.
- Wright, S.J. (1983) The dispersion of eggs by a bruchid beetle among *Scheelea* palm seeds and the effect of distance to the parent. *Ecology*, **64**, 1016–1021.
- Wright, S.J. (2002) Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia*, **130**, 1–14.
- Zhang, S.Y. & Wang, L.X. (1995) Fruit consumption and seed dispersal of *Ziziphus cinnamomum* (Rhamnaceae) by two sympatric primates (*Cebus apella* and *Ateles paniscus*) in French Guiana. *Biotropica*, **27**, 397–401.
- Zobel, M., Otsus, M., Liira, J., Moora, M. & Möls, T. (2000) Is small-scale species richness limited by seed availability or microsite availability? *Ecology*, **81**, 3274–3282.

Received 19 September 2002;
revision accepted 7 April 2003.