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How much is a lot? Seed dispersal by white-faced capuchins and implications for disperser-based studies of seed dispersal systems

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Abstract The quantity of seeds dispersed is considered one of several means to determine the dispersal effectiveness of an animal. However, there is little consistency in the manner in which quantities are measured or presented. Here, we quantify seed dispersal by white-faced capuchin monkeys (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica by measuring: degree of frugivory, number of plant species consumed, the number of seeds consumed per unit time, the number of seeds dispersed intact per unit time, and the number of seeds dispersed intact per unit space. Forty-nine percent of *C. capucinus* diet is composed of the fruit of 39 species, 4 of which constitute 82% of the frugivory. Seventy-four percent of consumed fruits contain seeds that pass intact through the capuchin digestive system. Capuchins pass a mean of 15.7 seeds of a mean of 1.3 species per defecation, and defecate 25.4 times per 12-h day. These numbers are compared with extant data for *C. capucinus*, and possible reasons for discrepancies among results between studies are discussed. We propose a standardization of quantitative measures of seed dispersal so that quantifications of seed dispersal can be compared within species, and eventually across species.

Keywords Seed dispersal · *Cebus capucinus* · Santa Rosa National Park · Comparative studies

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Introduction

Measuring the quantity of seeds dispersed by an animal is a critical initial step in understanding the dispersal ability of that animal (Lambert and Garber 1998). Schupp (1993, p 15) posits that "effectiveness, the contribution a disperser makes to plant fitness, depends on the quantity of seeds dispersed and the quality of dispersal provided each seed." Studies of seed dispersal by animals tend to focus on both the quantity of dispersed seeds, and the quality of dispersal (Chapman 1989; Kaplin and Lambert 2002; Stevenson 2000; Wrangham et al. 1994; Wehncke et al. 2003; Knogge et al. 2003). However, despite the recent plethora of research on seed dispersal by mammals, and specifically by primates, there is little overlap in the way in which quantity of seed dispersal is measured or reported.

Schupp (1993) suggests that the quantity of dispersal be measured as the number of visits made by a disperser (measured as the abundance of a disperser, disperser diet, and reliability of visitation) and the number of seeds dispersed per visit (measured as the number of seeds handled per visit and the probability of dispersing a handled seed). While these are excellent measures where the tree species is the unit of analysis (e.g., Balcomb and Chapman 2003), and/or the intention is to evaluate the relative effect of multiple dispersers on a single plant species (Herrera and Jordano 1981), in cases where the disperser is the unit of analysis (such as most primate-based studies of seed dispersal), and especially where the disperser exploits a wide variety of angiosperms, it would be beneficial to create a better measure of the effectiveness that one disperser has across multiple plant species. The latter is typically the way that seed dispersal is measured in primate studies (e.g., McConkey 2000). However, there exists little in the way of a standard comparative basis for measuring the quantitative effectiveness of one primate disperser species across multiple plant species. The development of a standard basis for comparison would be an important initial step in measuring the effectiveness of a disperser species and any subsequent effect on seed input and seedling recruitment. Quantifying seed dispersal is a critical initial step in understanding the long-standing relationship between fruiting trees and the animals that disperse them, and is the first in a series of variables linking animal behavior with forest composition.

There are numerous ways to measure the dispersal effectiveness of a single primate species vis-à-vis numerous plant species with regard to quantity of dispersal. These include: degree of frugivory, number of species consumed, the number of seeds consumed per unit time, the number of seeds dispersed intact per unit time, and the number of seeds dispersed intact per unit space. We propose a standardization of quantitative measurements where the animal, and not the angiosperm, is the unit of analysis, to serve as a basis of comparison across primate disperser species and between different populations of a given species.

We compare the values for the above measures from the current study of two groups of white-faced capuchin monkeys (*Cebus capucinus*), with the two prior studies of white-faced capuchin seed dispersal for which comparable information is reported: Chapman (1989) and Wehncke et al. (2003). While there are many other studies of seed dispersal by primates, our sample size in this comparative analysis is necessarily limited to the three studies (our own and those by Chapman and by Wehncke et al.) because they are the only ones that provide directly comparable data on seed dispersal by *C. capucinus*. We provide these comparisons to illuminate how differences in methodology can result in differences among findings. We describe the method for obtaining each result individually with respect to its reliability and relevance to the question of seed dispersal quantity. Additionally, we discuss variable results that arise from differences in length of study, sample size and site-specific fruit species availability.

It is important to note that methods of determining the quantity of seed dispersal by primates is just the start of measuring dispersal effectiveness, since issues of dispersal quality, spatial patterns of dispersal, and post-dispersal fate are also crucial to understanding the dispersal effectiveness of an animal (Howe and Smallwood 1982; Estrada and Coates-Estrada 1991; Chapman et al. 2003).

Methods

Study site and subjects

This study took place in Santa Rosa National Park, a 108 ha sector of the Area de Conservación Guanacaste (ACG) in northwestern Costa Rica, approximately 40 km south of the Nicaraguan border in Guanacaste province. Santa Rosa Park is home to several groups of habituated white-faced capuchin monkeys that have been studied since 1983.

Two habituated groups of white-faced capuchins were the focus of this study: the Cerco de Piedra (CP) group, composed of 19 individuals, and the Los Valles (LV) group, composed of 17 individuals. White-faced capuchins (*Cebus capucinus*) are arboreal, diurnal omnivores. Their diet is composed of numerous species of invertebrates, vertebrates, fruits, flower buds, and flowers.

Data collection

Over the course of 8 months of study (May–July 2005 and January–May 2006), two programs of focal observation were conducted. To record fruit (and hence seed) consumption, and defecation rates, two observers conducted all-day focal follows ($N = 50$, 393.5 h) on all adult individuals in both groups ($N = 16$) between the hours of 5:00 a.m. and 6:00 p.m. Two observers continuously observed focal animals all day or for as long as possible (range 2 h 12 min to 12 h 53 min, mean follow time 7 h 43 min). We discarded focal follows that could not be maintained for longer than 2 h or in cases where the focal animal was not visible for greater than 10% of the entire possible number of observation hours. Focal follows of this length were possible due to three factors: (1) excellent visibility of the monkeys in tropical dry forest, where the canopy is lower than in wet forest; (2) 25 years of habituation of these study groups to close observation such that animals readily forage in the lower canopy, sometimes come to the ground and exhibit a very low flight distance to researchers; (3) the constant presence of two data collectors, one of whom watched the monkey while the other recorded data. We recorded behavioral and defecation data using a hand-held data logger (Psion Workabout MX). This device records time to the second each time an entry is made. We recorded location data using a handheld Geographic Positioning System (GPS).

Each time the focal animal fed on fruit, we recorded the tree species along with a number that corresponded to the number of trees of that species consumed during that focal follow. We considered a fruit-eating bout to begin the moment that the focal animal picked or bit the first piece of fruit, and ended when the focal animal left the tree, changed their behavioral state (e.g., began to eat insects, groom, rest), or when they continued to forage but did not pick or eat fruit for 30 s. We recorded a waypoint using the GPS for each tree at which the focal animal consumed fruit, with the same name and number as was recorded in the data logger.

Each time the focal animal defecated, we recorded the defecation event and number in the data logger, took a waypoint, and collected the defecation in a labeled vial. We brought fecal samples ($N = 549$) to the field laboratory, where we identified each species of seed based on fruit samples taken during the focal animal follows. We then counted all seeds and recorded their species and number, and any visible damage.

For the second program of focal sampling, we collected general behavioral data (Rest, Social, Travel/Forage, Insect Feed, Vertebrate Feed, Fruit Feed, Drink, and Other) during half-hour focals to determine activity budgets ($N = 171$ activity budget focal animal samples, 85.5 h). When the focal animal was out of sight of both observers, this was recorded, and in cases where this exceeded 10% (3 min) of the half-hour focal time, we discarded the sample. This second program of sampling took place with the focal animal of the day. All activity budget samples began and ended on the hour or half-hour to help ensure the equal distribution of sampling times throughout the day.

Data analysis

We determined the degree of capuchin frugivory in two ways. Firstly, we extracted the duration of all recorded behaviors from the half-hour focal animal samples ($N = 95$ sessions, 47.5 h) and converted them to time in seconds. We then arrived at a final percentage score for each individual monkey, and then averaged these scores for the wet season (May–July 2005) and for the dry season (January–May 2006). We then compared totals to the percentage of time spent feeding on fruit for both groups, vis-à-vis all other activity categories (Rest, Social, Travel/Forage, Insect Feed, Vertebrate Feed, Drink and Other) to determine the amount of observation time spent feeding on fruit per day.

Secondly, we identified each event of feeding on any item in the half-hour focal animal samples, and converted the duration to seconds. We then calculated a percentage of time spent feeding on fruit vis-à-vis all feeding events by dividing the total number of seconds spent feeding on fruit by the total number of focal seconds spent feeding on all items (minus any out-of-sight time), and then arrived at a final percentage score for each individual monkey. We then averaged these scores for the wet season (May–July 2005) and for the dry season (January–May 2006) to determine the amount of feeding time spent feeding on fruit.

We determined the number of seed-bearing species consumed and passed intact by counting each seed-bearing species consumed during the course of the all-day focal animal observation. The number reported here is an underestimate as it was not possible to determine the individual species of the nine individual trees of the Genus *Ficus*, as well as seven fruiting tree species that were consumed by focal animals but were not identified. Here, all species of unidentified trees are referred to as one species, as are all individuals of the Genus *Ficus*.

We extracted the number of seeded species passed intact from the laboratory data. We then arrived at a percentage of seeded species observed to pass intact by dividing the total number of seeded species where at least one seed had been observed to pass intact by the total number of seeded species consumed.

We extracted the number of seeds passed per defecation as well as the number of species passed per defecation from the laboratory data. We arrived at a mean, median, and range for both the number of seeds per defecation as well as the number of species per defecation. An accurate count was possible for all species with the exception of species of the Genus *Ficus* and *Cecropia peltata*. Seeds of these species are too small (<2 mm in diameter) and usually too numerous to accurately count. Additionally, they are extremely delicate and are damaged very quickly by human manipulation. Thus, results pertaining to the number of seeds passed per defecation are underestimates, as they do not account for the very numerous seeds of the aforementioned species.

We determined the percentage of total defecations ($N = 549$) containing intact seeds and the percentage of total defecations that contained one, two and more than two species of seeds. We determined the frequency of defecation by calculating the time between two focal animal defecations. In cases where the focal animal was not visible by at least one observer for the entire time between two witnessed defecations, the record was not used. We then calculated the average time between defecations across all individuals. We then extrapolated the rate of seed dispersal by multiplying the average number of seeds dispersed per defecation by the average number of defecations per day.

We determined gut retention time by counting back from a defecation event to that species of tree in the case of rare fruit consumption. Whenever a focal animal consumed a species of fruit that had been eaten only once during the day, the time between fruit consumption and seed defecation was determined by counting the minutes between the two events ($N = 373$).

During all-day focal animal follows, observers recorded a waypoint every 30 min on the hour and half hour. We then combined these waypoints (1,344 for CP group, 974 for LV) for a 12-month period spanning May 2005–May 2006, and determined a home range for each of the two monkey groups using a 95% fixed kernel (in ArcView 3.2, Animal Movement 2.04). We determined density by dividing the total number of capuchins inhabiting that range (CP = 18, LV = 17) by the total area of each home range (CP = 102.87 ha, LV = 175.58 ha), and deriving a mean of those two numbers.

Results and discussion

Results of this study

From the half-hour sample data, the CP and LV groups spent 14% of all observation time feeding on fruit. The percentage of total feeding time spent feeding on fruit is 49%.

The average number of fruit species consumed per all-day focal animal follow across both seasons is five (median 5, range 1–9), and the average number of individual fruit-bearing trees of any species visited per all-day focal animal follow is 14 (median 13, range 2–26). Therefore a new fruit-bearing tree species is visited on average every 93 min, and fruit of any species is consumed on average every 33 min. Over the course of a 12 h day, this yields a daily average of 7.8 species consumed per day, and 21.8 individual fruiting trees exploited per day.

Both capuchin groups consumed the fruit of 39 different seed-bearing plant species. We found seeds from 29 (74%) of these plant species intact in capuchin feces. Of the ten species whose seeds were not observed to be passed intact in capuchin feces, five species have very large seeds that are spit out by capuchins, four species contain wind-dispersed seeds that are preyed on (chewed) by capuchins, and one species was observed to be eaten by a focal animal on only one occasion, and observer contact with the focal animal was lost before the seeds would have had time to be passed through the gut.

Of the observed defecations ($N = 549$), 408 (74%) contained intact seeds, whereas 141 (26%) did not. Fifty-two percent of fecal samples ($N = 281$) contained intact seeds of one plant species, 26% ($N = 111$) of fecal samples contained intact seeds of two species, and 4% ($N = 16$) of fecal samples contained intact seeds of more than two plant species.

White-faced capuchins defecate frequently. The mean time between defecations is 28 min (median 23 min, range 0.2–292 min). Over the course of a 12 h day, this yields an average of 25.4 defecations per animal per day. Our study animals defecate seeds an average of 138 min after ingestion (median 118 min, range 37–355 min). This is comparable to extant estimates of capuchin gut retention time (mean 94 $\pm$ 43 min, Wehncke et al. 2003).

Of the fecal samples containing countable seeds ($N = 349$), the average number of seeds of any species passed intact (not including seeds of the Genus *Ficus* and seeds of *Cecropia peltata*) per defecation is 15.7 (median 8, range 1–107). Of all fecal samples containing seeds ($N = 408$), the average number of plant species per defecation is 1.3 (median 1, range 1–4). The four most commonly passed seed species accounted for 82% of all defecated seeds ($N = 5{,}481$, excluding *Ficus* and *Cecropia*): *Genipa americana* ($N = 1{,}351$, 25%), *Acacia collinsii* ($N = 1{,}015$, 19%), *Casearia arguta* ($N = 1{,}431$, 26%), and *Sciadodendron excelsum* ($N = 635$, 12%).

Given the average number of countable seeds per defecation (15.7) and the average number of defecations containing seeds per day (18.8), an individual animal can be expected to pass intact an average of 295 intact seeds per day. Extrapolated to the 36 members of both our study groups, the average daily dispersal of countable seeds by both CP and LV group is 10,620.

Cumulative white-faced capuchin home ranges at this site are 102.87 ha for CP, and 175.58 ha for LV. White-faced capuchin density is 0.175 animals per hectare in CP's home range, and 0.097 animals per hectare in LV's home range.

Comparison with prior studies

Here we compare the results of our study to two sets of published results on white-faced capuchins: Colin Chapman's study in Santa Rosa National Park, Costa Rica (Chapman 1989), and Elizabeth Wehncke's study on Barro Colorado Island and the Summit Zoo, Panama (Wehncke et al. 2003). The results from the current study vis-à-vis the two other extant studies are in some cases disparate and in some cases very similar (Table 1). These discrepancies, discussed in detail below, result from differences in methodology, as well as differences in the duration and location of the study, and they highlight the need for a standardized set of measurements in frugivore-based studies of seed dispersal.

Degree of frugivory

Percentage of fruit in the diet of capuchins can be measured as either the percentage of total time spent feeding on fruit per total observation time, or as a percentage of time spent feeding on fruit per total time spent feeding. Differences in the way in which percentage of fruit in the diet is measured will produce vast differences in results. For example, in this study, white-faced capuchins spent 14% of all *observation* time feeding on fruits, but 49% of all *feeding* time feeding on fruits. Because time spent feeding on fruit as a percentage of total time spent feeding can be skewed by species-specific differences in nutritional intake, we propose that cross-species and cross-population comparison of frugivory be focused on the percentage of observation time spent feeding on fruit. A standardized set of measures would allow for analyses of differences in the degree of frugivory within species. However, differences in the degree of frugivory can also be the result of inter-annual differences in availability and successional changes in the forest (Chapman et al. 2002). Long-term, horizontal

Table 1 Comparison of the results of three seed dispersal studies of *Cebus capucinus*

	Wehncke et al. 2003	Chapman 1989	Current study
Fruit in diet (%)	53[a]	81.2[b]	14[a], 49[b]
Number of plant species consumed	95	41	39
Percentage of plant species passed intact	71% (67/95)	34% (14/41)	74% (29/39)
Mean number of seeds per defecation	NA[c]	NA	15.7 ($N = 349$, median = 8)
Mean number of species per defecation	2 ($N = 174$)	NA	1.3 ($N = 349$, median = 1)
Number of defecations per animal per day	8–10	NA	25.42
Animal density	NA	NA	CP: 0.175 ha^{-1}; LV: 0.097 ha^{-1}; Mean: 0.136 ha^{-1}
Percentage of defecations containing seeds	93% (161/174)	100% (28/28)	74% (408/549)
Duration of study (months)	4	26	8
Number of fecal samples analyzed	174	28	549
Study site	Barro Colorado Island, Panama	Santa Rosa National Park, Costa Rica	Santa Rosa National Park, Costa Rica

[a] Calculated as the percentage of total observation time spent feeding on fruits

[b] Measured as the percent of all feeding time spent feeding on fruits

[c] Data not available

datasets would be required to examine the exact impact of these on the degree of primate frugivory.

Number of plant species consumed

There is discrepancy between the three studies with regard to the number of plant species consumed. The two studies at the same site (Santa Rosa) produced effectively the same number of plant species whose fruit was eaten [current study and Chapman's (1989) study, 39 and 41 species respectively, Table 1], while on Barro Colorado Island (Wehncke et al. 2003), more than double the number of plant species were observed to be consumed by white-faced capuchins in only half the time of the present study (4 vs 8 months) and less than one-sixth the time of the Chapman study (26 months).

Percentage of species passed intact

The percentage of plant species whose seeds are passed intact is a measure of the efficacy of a frugivore as a disperser. However, here as elsewhere, there are discrepancies in results. The difference seems to be due to the numbers of fecal samples collected. Despite the fact that both the current study and Chapman's study took place at the same field site, and that similar numbers of plant species were observed to be consumed, the percentage of plant species whose seeds were observed to pass intact is different between these studies (74% and 34%, Table 1). Given the similar conditions of the studies, it is likely that these differences are a result of the number of fecal samples collected (549 vs 28). Because of seasonal variation in fruit consumption and seed defecation, a low number of fecal samples can result in sampling error. One means of dealing with large differences in the number of fecal samples collected (as above) would be the use of accumulation curves and rarefaction analysis.

Defecations containing seeds

The percentage of defecations containing intact seeds is a reliable way to estimate the quantity of seed dispersal. This measure can be combined with animal density measurements, number of defecations per animal per day, and the number of seeds and seed species per defecation to estimate seed fall in a given area. There are differences among results for the three studies, but these do not correspond to site differences or differences in the duration of studies. They do, however, correspond to differences in number of fecal samples obtained (Table 1). In the case of the fewest number of fecal samples (28) we see the highest percentage of defecations containing intact seeds, and in the study with the highest number of fecal samples (549), we see the lowest percentage of defecations containing seeds. This discrepancy is likely the result of sampling error.

Frequency of defecation

The number of defecations per animal per day in the current study is more than twice the upper limit in the study of

Wehncke et al. (2003) (8–10 vs 25.42 defecations per animal per day, Table 1). This is likely the result of differences in sampling method. During the course of this study, individual animals were followed for several hours at a time, and all defecations recorded. In Wehncke's study, defecation rates per day were estimated based on shorter periods of focal animal sampling. Consecutive defecation events over long periods of time were not recorded, which may have led to an underestimation of the rate of defecations per day due to daily variation in defecation frequency as well as variation in time between defecations, which can range considerably.

Seeds and species per defecation

The number of seeds and seed species per defecation is another measure of the quantity of seed dispersal, and it can be combined with the number of defecations per day and the number of animals per area to estimate seed fall in a given area. It is also a relatively easy aspect to measure, as seed counting and identification is usually done in the course of seed dispersal studies for other reasons (e.g., germination experiments). Here, while there are no comparative data available for the average number of seeds per defecation, Wehncke's mean of two seed species per defecation is relatively consistent with the present study's result of 1.3 species per defecation.

Animal density

The mean density of the two capuchin groups studied here is 0.136 animals per hectare. This is an important aspect in determining seed fall in a given area, and can be used to aid in establishing a comparative basis for seed rain between conspecific frugivores as well as within species and between sites. Capuchins disperse numerous intact seeds of multiple species each day as a consequence of their high rates of defecations per animal per day, their large group sizes, the frequency of seed occurrence in the feces, and the high number of seeds per defecation. However, the numbers here are underestimates. Seeds of the species *Cecropia peltata*, as well as those of the Genus *Ficus*, were not counted due to the difficulty of separating and counting individual seeds. Seeds of these species are <2 mm in diameter, and are deposited in capuchin feces in very high numbers. The quantity of seed input by capuchins is thus not used here as a point of comparison because of the difficulty of accurately gauging the number of very small and fragile seeds dispersed.

Conclusion

White-faced capuchin monkeys disperse numerous seeds of multiple plant species. However, given the dearth of standardized measures of seed dispersal quantity, it is difficult to put these numbers into context. While the quantity of seeds dispersed by a primate is only one of several measures of disperser effectiveness—which include qualitative measures such as seed handling and gut passage, and spatial measures such as dispersal distance and the suitability of defecation locations for seed germination and seedling growth—it is an important initial step in measuring the effectiveness of a disperser.

Reliable and easily comparable measures of the quantity of dispersed seeds are: the percentage of fruit in the diet (measured as the percentage of time spent feeding on fruit per total observation time), the number of plant species consumed, the percentage of plant species whose seeds are passed intact, the number of seeds and species per defecation, the number of defecations per animal per day, animal density, and the percentage of defecations containing seeds. Standardizing these measures will allow for the comparison of the effectiveness of primates as seed dispersers both between species, and between different populations of the same species.

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