

Effects of Gut Passage, Feces, and Seed Handling on Latency and Rate of Germination in Seeds Consumed by Capuchins (*Cebus capucinus*)

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ABSTRACT One of the key measures of the effectiveness of primary seed dispersal by animals is the quality of seed dispersal (Schupp: *Plant Ecol* 107/108 [1993] 15–29). We present data on quality of seed dispersal by two groups of white-faced capuchins (*Cebus capucinus*) in Costa Rica to test the hypothesis that capuchin seed handling results in effective primary dispersal for some fruit species they consume. We examined seed handling for 27 plant species, and germination rates of 18 species consumed by capuchins. For five of the most commonly swallowed seed species, we determined germination rates and average time to germination (latency) for seeds ingested and defecated by capuchins and compared these

to seeds removed directly from fruit and planted. For the same five species, we compared germination rates and latency for passed seeds planted in capuchin feces to those cleaned of feces and planted in soil. For three of five species, differences in proportion of germinated seeds were significantly higher for gut passed seeds than for controls. For four of five species, germination latency was significantly faster for gut passed seeds than for controls. Feces had either no effect on seed germination rate or precluded germination. Data presented here support the hypothesis that white-faced capuchins are effective primary dispersers. *Am J Phys Anthropol* 138:486–492, 2009. © 2009 Wiley-Liss, Inc.

Recent studies have established the importance of primates as seed dispersers, and as a result, their role in the maintenance and regeneration of tropical forests (Chapman and Onderdonk, 1998). Primates comprise between 25 and 40% of frugivore biomass in tropical forests (Chapman, 1995), and defecate or spit large numbers of viable seeds (Lambert, 1999), which makes them particularly well suited to be effective dispersers. Numerous primate species exhibit morphological and behavioral adaptations that enable them to successfully exploit fruit (Lambert and Garber, 1998), and primate fruit preferences for certain suites of fruit traits have been documented (Stevenson, 2004).

Measuring the quality of seed dispersal by an animal is a critical initial step in understanding the dispersal effectiveness of an animal. Disperser effectiveness, or the contribution an animal makes to plant fitness, depends on “the quantity of seeds dispersed and the quality of dispersal provided each seed” (Schupp, 1993). Here, we focus on the latter. Although the quantity component of seed dispersal effectiveness (*sensu* Schupp, 1993) refers to the total number of seeds removed from a parent plant, factors influencing the quality component of seed dispersal effectiveness include seed handling, gut passage, and dispersal site attributes (Kaplin and Moermond, 1998; Vander Wall and Longland, 2004; Verdu and Traveset, 2004; Rodriguez-Perez et al., 2005; Loiselle et al., 2007; Schupp, 2007; Traveset et al., 2007). In this article, we evaluate the quality component of capuchin seed dispersal in order to evaluate their effectiveness as dispersers in dry tropical forests.

The most preliminary measure of disperser quality is seed handling. That is, does an animal’s initial treatment of a seed destroy or enhance its chance for sur-

vival? Numerous studies of seed dispersal have documented initial seed fate after seed handling (e.g., Kaplin and Moermond, 1998). Treatment of seeds can range from the destruction of seeds by the animals that eat them through chewing, biting, pecking and so forth, such that those seeds are no longer viable, (Overdorff and Strait, 1998) to careful de-fleshing followed by spitting of seeds (Kankam, 2000) to the swallowing and intact passage of seeds (Rowell and Mitchell, 1991). Previous studies document that capuchin seed handling consists mainly of swallowing seeds whole and defecating them intact (Chapman, 1989; Rowell and Mitchell, 1991; Wehncke et al., 2003; Valenta and Fedigan, 2008).

An additional measure of the quality of a disperser is the effect of passage through the intestinal system after a seed has been swallowed. Endozoochorous dispersal

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exposes seeds to digestive fluids during gastrointestinal passage, which can result in mechanical and/or chemical scarification of the seed coat (Traveset et al., 2007). Additionally, the separation between pulp and seeds that occurs during this process can result in deinhibition, or the removal of osmotic pressure, light-blocking pigmentation, and secondary metabolites that may inhibit germination (Traveset et al., 2007). Some studies have shown that gut passage neither helps nor hinders a seed's chance of germinating (Knogge et al., 2003). In other cases, passage through an animal's digestive system appears to greatly increase germination rate (Chapman et al., 1992), which we define as the proportion of germinated to planted seeds. Previous studies document that passage through the capuchin intestinal system does not preclude germination (Chapman, 1989; Wehncke et al., 2003; Smith, 2004) and for some species results in increased germination vis-à-vis seeds that are not subject to gut passage (Wehncke and Dalling, 2005).

In addition to altering the rate of germination, gut passage may have an effect on germination latency, which we define as the number of days that elapse between seed deposition and germination. Previous studies demonstrate that even in cases where germination rates are not affected by gut passage, germination latency can be (Knogge et al., 2003). In a study at Santa Rosa National Park, Chapman (1989) found that 80% of all seeds left in primate feces were removed within 1 week after initial deposition. It is possible that seeds are safely redeposited in locations suitable for germination and growth, and there is evidence that in certain systems, secondary dispersers are as critical to the process of dispersal as primary dispersers (Vander Wall and Longland, 2004). Indeed, multiple relocations of seeds are possible after primary dispersal takes place (Vander Wall and Longland, 2004). But in some cases, seeds are victims of secondary seed predation (Forget and Wenny, 2005). In the latter case, reduced germination latency would allow seeds to escape seed predators and potentially increase the likelihood of a seed surviving to the next stage. Additionally, for some species, faster germination latency is predictive of increased seedling survival, growth and fecundity (Verdu and Traveset, 2005), and seedling size (Garwood, 1986). Also, in situations of competition for light or other resources, reduced germination latency may be of critical importance (Miller et al., 1994). In other cases, however, longer germination latency can reduce seed mortality, via the avoidance of unsuitable conditions, competition, and seasonal hazards (Verdu and Traveset, 2005). Previous studies of the effect of capuchin gut passage indicate that, at least for some species, germination latency after capuchin gut passage is faster than for seeds removed directly from fruit (Wehncke and Dalling, 2005).

Another potential predictor of germination rate and latency is the effect of feces on germination. The fecal matrix surrounding a deposited seed can either enhance or impede seed germination and seedling survival, via the chemical composition of feces, moisture content and retention, and the presence of phenolic compounds and fatty acids that can act as germination inhibitors (Stiles, 2000; Traveset et al., 2007). Subsequent seedling growth can also be affected due to the fertilizing effect of remaining fecal material (Traveset and Verdu, 2002). Germination latency can also be affected by the presence of feces (Cosyns et al., 2005). Traveset et al. (2001) found

that differences in animal and vegetable matter ratios resulted in differences in both seed germination rate and seedling survival. The chemical and moisture content of animal feces may thus affect both germination and seedling survival and growth. Postdispersal, the presence of feces can also result in variations in predator detection and seed damage (Lambert, 2002; Lambert and Chapman, 2005). To date, results for post-capuchin-dispersal seed fate have been mixed (Chapman, 1989; Wehncke and Dalling, 2005), and information on the effect of the presence of capuchin feces on germination rate and latency is lacking.

Thus far, existing data suggest that white-faced capuchins are effective primary seed dispersers: they disperse large numbers of seeds of multiple species (Valenta and Fedigan, 2008), swallow and defecate seeds intact (Rowell and Mitchell, 1991) and passage through capuchin digestive systems does not preclude, and in some cases increases, seed germination (Wehncke and Dalling, 2005). Here, we further test the hypothesis that capuchin frugivory results in effective primary seed dispersal by examining several aspects of the quality of seed dispersal by white-faced capuchins in a tropical dry forest. Specifically, we examine capuchin seed handling, as well as the effects of capuchin seed handling, gut passage, and feces presence on the germination rate and latency of dispersed seeds. Based on previous studies of white-faced capuchin seed handling (Chapman, 1989; Rowell and Mitchell, 1991; Wehncke et al., 2003; Valenta and Fedigan, 2008), we predict that seed handling by our study animals will consist mainly of passing seeds intact rather than spitting them out or destroying them via chewing. We also predict that passage through the capuchin intestinal system will result in increased rates and decreased latency of seed germination. And finally, since previous studies of the effects of feces on seed germination have produced mixed results (Traveset et al., 2001), we predict that the presence of a fecal matrix around deposited seeds will enhance germination rates and decrease latency to germination due to the chemical and moisture content of capuchin feces.

METHODS

Study site and subjects

This study took place in the Santa Rosa sector of the Area de Conservacion Guanacaste, a 110,000 hectare reserve of regenerating tropical dry forest, in the northwestern corner of Costa Rica, ~40-km south of the Nicaraguan border. Santa Rosa Park is composed of fragments of deciduous, semievergreen and riparian forest, as well as regenerating pasture land. The dominant habitat in Santa Rosa Park is tropical dry forest, with most trees losing their leaves in the distinct dry season during which time little to no rain falls (Janzen, 1983). The park is home to three species of nonhuman primate, including several habituated groups of white-faced capuchins (*Cebus capucinus*).

Two habituated groups were the focus of the current study: the Cerco de Piedra group, composed of 19 individuals, and the Los Valles group, composed of 17 individuals. All adults in both groups were observed for a total of 16 individuals. The two groups inhabit slightly overlapping home ranges.

Data collection

During 8 months of study (May through July, 2005 and January through May, 2006), covering parts of both the wet and the dry seasons, we collected behavioral data and fecal samples from adults in both study groups. We conducted behavioral observations in the form of all-day, continuous focal follows, between the hours of 5:00 AM and 6:00 PM ($N = 50$, 393.5 h). All monkeys were individually identifiable based on their age, sex, and individual markings. Each day, two observers would continuously observe one adult monkey all day or for as long as conditions made possible (range = 2 h 12 m up to 12 h 53 m, mean follow time = 7 h 43 m). We discarded data when focal sessions could not be maintained for longer than 2 h, or in cases where the focal animal was not fully viewed by at least one observer for greater than 10% of possible observation time.

We recorded behavioral and defecation data using a hand-held data logger (Psion Workabout MX). This device records time to the second. Location data of observations were recorded using a handheld Geographic Positioning System. All occurrences of fruit feeding were recorded, along with the tree species and, when possible, the treatment of the seed or seeds in each piece of fruit consumed as: 1) the fruit was swallowed whole; 2) the pulp was removed and the seed(s) spit out or dropped; 3) the seed was masticated and destroyed; 4) the fruit was picked and dropped; 5) some seeds in the fruit were swallowed whole, while some were spit out, masticated and destroyed, or dropped. Because many species of fruit contain multiple small seeds (<0.5 cm), the individual fruit (and not seed) is the unit of analysis.

Each time the focal animal defecated, we recorded the defecation event in the data logger, took a waypoint, and collected the defecation in a labeled vial. We returned fecal samples ($N = 549$) to the field laboratory, where we identified each species of seed from fruit samples that we had collected during the focal animal follows. We then counted and identified all seeds and recorded their species and number (except in the case of *Cecropia peltata* and seeds of the Genus *Ficus*, whose extremely small size—<0.2 cm—and delicacy made individual counts impossible). We examined seeds and recorded any visible damage.

Seeds that were handled by the focal animal and discarded (e.g., spat out, picked and dropped) were also collected and returned to the field laboratory for planting. We extracted the number of records of each category of seed treatment from the data logger and determined the percentage of records for each category across all species and for each individual species.

We planted all collected seeds in one of a series of germination trials. Seeds of all treatments (gut passed and cleaned of feces, removed from fruit and cleaned, gut passed and left in the fecal matrix, cleaned of feces and placed in a soil matrix, spit, picked and dropped, masticated) were planted on top of florist's foam in order to control for over- and under-watering. Treatments were watered whenever the florist's foam became dry to the touch. We placed these in clean Petri dishes, watered them as needed, housed them in a screened outdoor enclosure with natural light, and checked daily for germination.

Seeds of the five most commonly encountered species (*Genipa americana*, *Sciadodendron excelsum*, *Trichilia martiana*, *Acacia collinsii*, and *Casearia arguta*) were

planted in two different experimental treatments to determine the effect of gut passage and feces on germination rate and latency.

To test the effect of gut passage on germination rate and latency, we cleaned all feces from a portion ($N = 870/1,984$) of gut passed seeds and planted them alongside controls: conspecific seeds removed directly from ripe fruit and cleaned of all pulp ($N = 1,028$).

To test the effect of white-faced capuchin feces on germination rate and latency, we left another portion ($N = 619/1,984$) of gut passed seeds of the five species in the feces in which they had been deposited and collected. We planted these alongside controls ($N = 495$): gut passed seeds that we had removed from the same defecation, cleaned of feces and placed in soil collected from the exact location of that defecation. Typically in germination experiments where soil is used, controls are planted in sterile, high quality soil (e.g., Kankam, 2000). But in this case, due to the natural variation in soil quality at the study site (J.A. Klemens, pers. comm.) we decided to build the possible effect of that variation into the study. Additionally, we took seeds in both treatments in equal numbers from the same fecal samples, to avoid bias introduced by differences in gut passage time and fecal matrix.

Additional seed species that were collected from feces ($N = 3,157$ seeds of the 18 species handled by capuchins for which samples were obtained) were cleaned of feces, planted on top of florist's foam in Petri dishes, watered as needed, and checked daily for germination. We compared the germination rates of these seeds to seeds that had been handled but not passed by capuchins (spit, picked and dropped, masticated), and with seeds removed directly from fruit and cleaned of fruit pulp.

Data analysis

We analyzed all germination rate data using a Proportion of Difference Analysis (Freund and Simon, 1997). Where z exceeds 2.33, the difference between proportions is greater than expected by chance at a Bonferroni-corrected α of 0.01.

We analyzed germination latency by calculating a mean number of days to germination for each species in each treatment, which we then compared using a Test for Differences Between Means (Freund and Simon, 1997). Where z exceeds 1.96 the null hypothesis is rejected, and the difference between means is considered to be greater than expected by chance at a Bonferroni-corrected α of 0.01 for the gut passage test and 0.017 for the feces test.

RESULTS

Seed handling

White-faced capuchins swallowed all seeds in 34% ($N = 3,596$) of observed fruit feeding events. In 34% of observed fruit feeding events capuchins swallowed some seeds in fruit whole, and spit out, masticated or dropped the rest. In 17% of all observed fruit feeding events, seeds were spat out, but this treatment was limited to 9 of the 27 species. In 9% of records, fruits were picked and then dropped. In only 6% of observed fruit feeding events were seeds destroyed through chewing, and this was limited to 8 of the 27 species sampled.

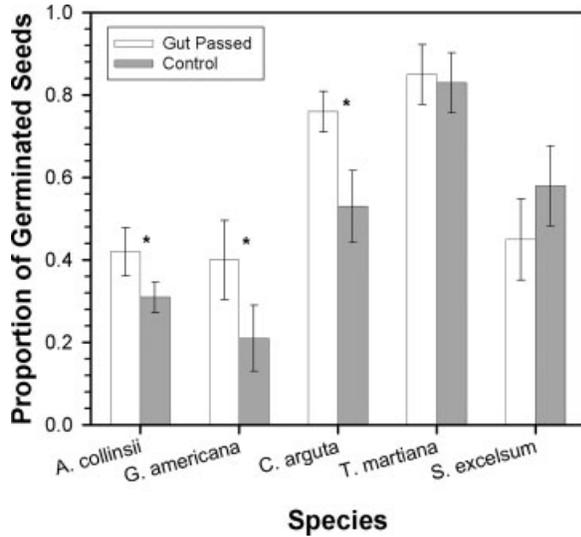


Fig. 1. The effect of gut passage on germination rates. Asterisks indicate significant differences between treatments (Bonferroni-corrected $\alpha = 0.01$). Proportion of germinated gut passed versus control seeds = *A. collinsii*, N1 = 118/282, N2 = 187/600; *G. americana*, N1 = 40/100, N2 = 21/100; *C. arguta*, N1 = 217/285, N2 = 66/125; *T. martiana*, N1 = 85/103, N2 = 85/103; *S. excelsum*, N1 = 45/100, N2 = 58/100.

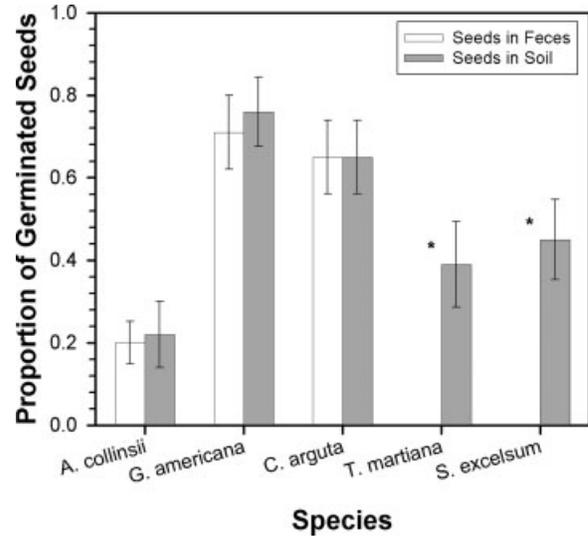


Fig. 3. The effect of feces on germination rates. Asterisks indicate significant differences between treatments. (Bonferroni-corrected $\alpha = 0.01$). Proportion of germinated seeds planted in feces versus seeds cleaned of feces and planted in soil = *A. collinsii*, N1 = 45/225, N2 = 22/101; *G. americana*, N1 = 70/100, N2 = 75/99; *C. arguta*, N1 = 71/110, N2 = 72/110; *T. martiana*, N1 = 33/85, N2 = 0/100; *S. excelsum*, N1 = 45/100, N2 = 0/100.

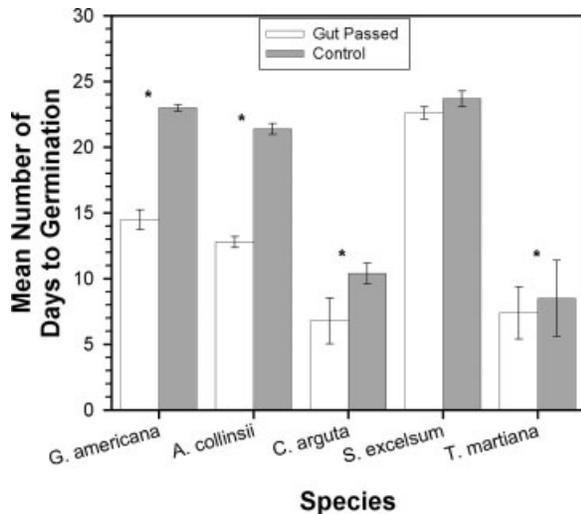


Fig. 2. The effect of gut passage on germination latency. Asterisks indicate significant differences between treatments. (Bonferroni-corrected $\alpha = 0.01$).

Effects of gut passage

For three of the five major plant species examined (*A. collinsii*, *C. arguta*, and *G. americana*), germination rates were significantly higher for gut passed seeds than for controls (*A. collinsii*, $z = 3.24$, $P < 0.001$; *C. arguta*, $z = 4.02$, $P < 0.001$; *G. americana*, $z = 2.92$, $P < 0.001$). For two species, there was no significant difference (*T. martiana*, $z = 0$, $P = 1$, *S. excelsum*, $z = 1.83$, $P = 0.03$) (see Fig. 1).

For four of the five major plant species examined, germination latency was significantly faster for gut passed

seeds than for controls (*G. americana*: 14.5 versus 23 days, $z = 3.72$, $P = <0.001$; *T. martiana*: 7.4 versus 8.5 days, $z = 2.76$, $P = 0.006$; *A. collinsii*: 12.8 versus 21.4 days, $z = 8.97$, $P = <0.001$; *C. arguta*: 6.8 versus 10.4 days, $z = 8.04$, $P = <0.001$). For the fifth species, there was no significant difference (*S. excelsum*: 23.7 days versus 22.6 days, $z = 0.26$, $P = 0.795$) (see Fig. 2).

Effects of fecal matrix

For two of the five most commonly swallowed species (*T. martiana* and *S. excelsum*), seeds planted in feces did not germinate at all; the germination rate of control seeds was significantly higher (*T. martiana*, $z = 7.06$, $P = <0.001$; *S. excelsum*, $z = 7.76$, $P = <0.001$). For three species, there was no significant difference (*A. collinsii*, $z = 0.375$, $P = 0.352$; *G. americana*, $z = 0.823$, $P = 0.206$; *C. arguta*, $z = 0$, $P = 1$). (see Fig. 3).

For one of the three feces-planted species that germinated, germination latency was significantly faster for controls (*G. americana*: 15.5 versus 21.4 days, $z = 5.25$, $P = <0.001$). For one species, germination latency was significantly faster for seeds planted in feces (*C. arguta*: 12.9 versus 14.8 days, $z = 3.29$, $P = <0.001$). For the third species, there was no significant difference (*A. collinsii*: 14.3 versus 15.6 days, $z = 0.631$, $P = 0.528$). (see Fig. 4).

Effects of all treatment categories across 18 plant species

The following results pertain to the 18 species that capuchins handled and for which it was possible to obtain samples for planting. Seeds of 17 of the 18 species that were processed by capuchins and planted were swallowed, one species was picked and dropped, three

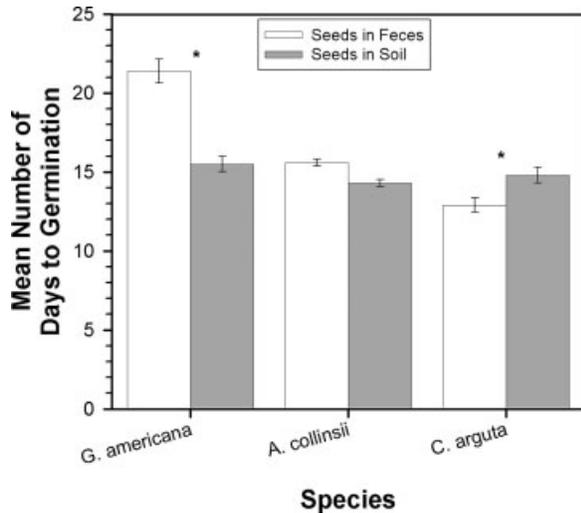


Fig. 4. The effect of feces on germination latency. Asterisks indicate significant differences between treatments. (Bonferroni-corrected $\alpha = 0.017$).

species were spit, and one species was masticated. Forty-nine percent of gut passed seeds germinated, compared to 32% of seeds removed directly from fruit, and 20% of spat seeds. No seeds that were picked and dropped or masticated germinated.

Of all monkey treatments across plant species, gut passage is the only treatment with a significantly higher germination rate than seeds removed directly from fruit (49% versus 32%, $N = 3,157$, $z = 9.44$, $P = <0.001$). Spit seeds across all species show a statistically significant decrease in germination rate of 12% compared to seeds removed directly from fruit ($N = 1,501$, $z = 3.24$, $P = <0.001$).

DISCUSSION

Data presented here are consistent with other studies of primate seed dispersal in the Neotropics and support the hypothesis that capuchin frugivory and seed handling result in effective primary seed dispersal for a subset of the fruit species they consume. Our prediction that capuchin seed handling would consist mainly of the intact passage of seeds was upheld. The most common form of seed treatment is ingestion (swallowing all seeds in a fruit and swallowing some of the seeds in a fruit together made up 68% of fruit treatment records), and across the 18 species that were planted in a controlled environment the highest germination rate occurs amongst swallowed seeds. Although we observed a few cases where capuchin seed handling completely precluded germination, these were confined to one species: *Sloanea terniflora*. We observed few instances of systematic seed destruction, and those few observed cases are confined to five species: *Guazuma ulmilfolia* (100% of records, $N = 6$), *Luehea alternifolia* (46%, $N = 136$), *Luehea candida* (83%, $N = 19$), *Lasciviasis negra* (100%, $N = 26$), *Lasciviasis ruscifolia* (70%, $N = 19$). *Luehea* species, which accounted for 75% of all cases of seed mastication, have a winged, wind-dispersed fruit. Capuchins masticated and destroyed many of the seeds of *Luehea* species, but by banging the mature, dehisced pods against hard substrates, they also released multiple

winged seeds into the air that they did not examine or consume. This behavior is most common during the plant's dispersal season in February–March (Haber and Frankie, 1983). Thus, for *Luehea* species, capuchins serve both as seed predators and potentially as primary seed dispersers for a subset of seeds.

Three of the five species analyzed here show a significant increase in germination rate when passed through the intestinal system of a capuchin. Thus, our prediction that passage through a capuchin's gut would increase germination rate was partially supported. In contrast, the presence of feces has either no effect on germination rate, or a significantly detrimental one, which is contrary to our prediction. The two species (*S. excelsum* and *T. martiana*) that did not germinate in the presence of feces are both species that fruit in the wet season, when (in stark contrast to the dry season) rainfall occurs on an almost daily basis (Coen, 1983), and fecal matter may be rapidly washed away. Therefore, while feces have a negative effect on germination rates for these two species, the effect of feces on germination in a controlled environment—at least for fruit consumed and defecated in the wet season—may not be a meaningful measure due to the rapid removal of feces in the field.

Additionally, the two species that did not germinate in feces were the only species in this sample that did not have increased germination rates when passed through the capuchin intestinal system. They also exhibit traits that have been proposed to belong to a bird dispersal syndrome, having small, unprotected, unhusked, brightly colored fruits (see Janson, 1983; Link and Stevenson, 2004). *S. excelsum* produces small (mean width = 7.1 mm, $N = 102$) bright purple fruit, which contains multiple seeds (mean = 8, $N = 24$) that are paper-thin and extremely small (<2 mm in all dimensions). *T. martiana* produces yellow seed pods that dehisce to reveal small seeds (mean width = 4.2 mm, $N = 206$, mean number of seeds per pod = 4.8, $N = 27$) covered in a brilliant red aril.

The remaining three species (and those for which gut passage increases germination rate) exhibit traits that have been proposed to belong to a mammal-dispersal syndrome (Ibid.). *G. americana* and *C. arguta* have large, pale greenish-yellow fruit with very tough outer skins that contain multiple, large seeds. *A. collinsii*, while producing only a few small seeds per fruit (mean width = 2.76 mm, $N = 200$, mean number of seeds per fruit = 7.78), is heavily protected by sharp thorns that provide highly aggressive *Pseudomyrmex* ants shelter in exchange for predator protection. This ant-acacia mutualism is one that has long been studied by ecologists (Young et al., 2008), and is rarely interrupted by frugivores. During the course of this study, the white-throated magpie jay (*Calocitta formosa*) was the only other species observed to consume the fruit of *A. collinsii*. Because these birds avoid landing on the branches, they were rarely successful in pecking out the yellow-arillated seeds from their pods. For these birds, *A. collinsii* consumption was limited both by the difficulty of this method of foraging as well as by the constraint of foraging on only those seed pods that had dehisced. Capuchins, on the other hand, are able to remove and open nondehisced seed pods, by overcoming and ignoring ant defenses, while consuming large amounts of *A. collinsii* fruit (Ibid.).

The effect of feces and gut passage on germination latency follows the same pattern as the previously

described effect of each on germination rate: increased germination latency when planted in feces, and decreased germination latency for gut passed seeds. In the three species for which feces does not preclude germination, latency was significantly faster for one species (*G. americana*) when planted in soil than when planted in feces. Here, as with germination rate, the presence of feces had a negative or minor effect on germination latency for all species.

Four out of five species show significantly faster germination latency when passed through the capuchin intestinal system than when removed from fruit. Interestingly, the species (*S. excelsum*) that does not show significantly faster germination latency with gut passage also does not show increased germination rates with gut passage, and did not germinate at all when planted in feces. Here, as with germination rates, gut passage markedly reduces germination latency in three species (*A. collinsii*, *G. americana*, and *C. arguta*), but has a relatively minor effect on the fourth, *T. martiana* (7.4 versus 8.5 days).

Several studies have established the importance of primates as seed dispersers, and as a result, their important role in the maintenance and regeneration of tropical forests. One such study in Uganda demonstrated a markedly lowered rate of seedling recruitment in areas where primate seed disperser populations were reduced, compared to intact frugivore communities (Chapman and Onderdonk, 1998). Similar findings for black lemurs in Madagascar, led to the conclusion that if lemur populations decrease, "a large proportion of the tree species would suffer from reduced seed dispersal (which) could lead to their poor regeneration and, with time, a change in the plant species composition of the forest" (Birkinshaw, 1999: p. 197). Thus, frugivorous primates may be critical to the regeneration, maintenance, and survival of at least some of the fruiting trees that sustain them (Chapman and Chapman, 1996). To understand the extent to which primates influence forest regeneration and maintenance is not only central to understanding primates in an ecological context; it is also critical to understanding the potentially important effects that their behavior and choices exert on the ecosystems in which they live. Measuring the quality of primary dispersal provided each seed is an important preliminary step in understanding disperser effectiveness.

In most cases, capuchins swallow seeds whole and pass them intact, and, for the seed treatment types and species considered here, this form of seed handling resulted in the highest rates of germination vis-à-vis other treatments. In four of the five cases examined here, seed ingestion and defecation also reduced germination latency. Therefore, in terms of these measures of quality and for these commonly consumed fruit species, we conclude that white-faced capuchin monkeys are effective primary dispersers.

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