Effect of Different Primate Species on Germination of *Ficus* (*Urostigma*) Seeds

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We examined the germination of *Ficus* seeds (subgenus *Urostigma*) after defecation by six primate species (New World monkeys, Old World monkeys, and apes). Seeds from figs (control) and primate feces were placed in a thermostatically controlled chamber for 30 days. Seeds defecated by *Alouatta palliata*, *A. pigra*, and *Cercopithecus aethiops* showed significantly higher germination rates than control seeds. In addition, seeds from *A. palliata* feces germinated significantly faster than control seeds and seeds from *C. aethiops* and *Pan troglodytes*. These differences may be due to the different digestive characteristics of the six primate species. Zoo Biol 23:273–278, 2004. © 2004 Wiley-Liss, Inc.

Key words: New and Old World monkeys; apes; figs; seed germination experiment

INTRODUCTION

Some studies have suggested that figs (*Ficus* spp., Moraceae) play a keystone role in neotropical and paleotropical forests [Janzen, 1979; McKey, 1989; Nason et al., 1998] (but see Gautier-Hion and Michaloud [1989]) because they exhibit heavy fruit production, aseasonal patterns of reproduction, and high calcium levels [O'Brien et al., 1998], and are considered able to sustain frugivores throughout

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periods of general food scarcity [Terborgh, 1986]. This makes *Ficus* "the most important plant genus for tropical frugivores" [Shanahan et al., 2001, p. 529].

Both Old World and New World primates (e.g., chimpanzees [Wrangham et al., 1994], orangutans [Nowak, 1999], baboons [Lieberman et al., 1979], guenons [Lambert, 2002], and howler monkeys [Andresen, 1999]) feed on figs. Various studies [Lyon and Horwich, 1996; Chapman and Onderdonk, 1998] have highlighted the role of primates as dispersers of *Ficus* seeds. In some cases, primates can increase fig seed germination after ingestion [Wrangham et al., 1993; Bravo et al., 1995; Stevenson et al., 2002]. Nevertheless, some studies have shown no significant difference between germination of ingested and control seeds [Bravo and Zunino, 2000; Stevenson et al., 2002]. Furthermore, Julliot [1996] found that ingested seed germinated less than control seeds. The differences in dimensions, proportions, and morphology of the digestive tract of different primate species influence food retention time in an animal's gut [Lambert, 1996], and in turn can affect seed germination capacity. Variations among the results of previous studies probably reflect the different *Ficus* species used and the conditions under which the germination experiments were carried out [Traveset, 1998].

We evaluated the effect of six primate species on germination of *Ficus* (*Urostigma*) seeds by analyzing the differences in the germination of seeds ingested by the six primate species, and in ingested vs. noningested seeds. Seed passage times through the digestive tract of the same primate species were also determined.

Mature syconia of *Ficus* (*Urostigma*) perforata and *F. pertusa* (diameter = 0.9 ± 0.01 and 0.8 ± 0.2 cm, respectively) were collected in July 1999 in Playa Escondida in southern Veracruz ($18^{\circ} 35' N, 95^{\circ} 03' W$) and Rancho Pilancones in central Veracruz ($20^{\circ} 12' N, 96^{\circ} 47' W$), Mexico, both of which are inhabited by troops of Mexican howler monkeys (*Alouatta palliata mexicana*). In each site we collected 200 g of syconia from each species. About 15 g of a mixture of figs of both species were air-dried to obtain seeds for controls, and the rest were placed in a refrigerator ($5^{\circ}C$) until they were fed to the primates. Since troops of howler monkeys were feeding on *Ficus* trees at the time we collected figs, feces containing fig seeds were collected and air-dried (to avoid fungi infestation).

For 1 week, figs were fed to five species of captive primates (two Old World monkeys (*Papio hamadryas* and *Cercopithecus aethiops*, Cercopithecinae), one New World monkey (*Alouatta pigra*, Atelinae), and two species of apes (*Pan troglodytes* and *Pongo pygmaeus*, Pongidae)) at the Africam Safari Zoo, Puebla, Mexico. Individuals (Table 1) of each species were randomly chosen and isolated in the cages they usually shared with conspecifics, to facilitate feeding and feces collection. Each individual was fed about 20 g of figs (a mixture of both species) twice a week, and the feces were collected every day and air-dried. We calculated the time required for the seeds to pass through the digestive tract of the animals, registering the time we fed the primates and the approximate time of seed defecation. The animals were checked at 60-min intervals, but only from 0900 to 1800 hr (i.e., when the Africam Safari Zoo is open to the public).

Both control seeds and seeds from dried feces were washed to separate them from other materials. Trials were performed with seeds from the feces of the six primate species, and seeds from syconia (control). All seeds were observed under a stereoscopic microscope, and those in which the embryos had been eaten by figwasps (Agaonidae) were discarded. Randomly selected viable seeds were placed on

Primates	NI	LC	FP (h)	SN	GS (%)	T ₅₀ (day)
New world monkeys						
Alouatta palliata mexicana		Wild	20.4^{a}	100	83	10.9 ± 1.4
Alouatta pigra	1	Zoo	23	100	73	15.4 ± 3.1
Old world monkeys						
Cercopithecus aethiops	6	Zoo	20	100	68	19.8 ± 4.1
Papio hamadryas	5	Zoo	14	50	64	16.8 ± 1.7
Apes						
Pongo pygmaeus	1	Zoo	30	100	55	14.8 ± 2.9
Pan troglodytes	5	Zoo	18	80	45	21 ± 6.6
Control seeds		_	_	100	36	25 ± 3.6

TABLE 1. Results of germination trials using *Ficus (Urostigma)* seeds collected from feces of six primate species and from syconia (control)

^afrom Milton [1984].

NI, number of individual fed with figs; LC, life condition; FP, time required for the passage of seeds through digestive tract; SN, number of seeds used for germination trials; GS, percentage of germinated seeds; T_{50} , time needed for 50% of seeds to germinate (±SD).

filter paper in petri dishes (10 seeds per dish). At the start of the experiment, the seeds were allocated to dishes as follows: 10 dishes for control seeds; 10 dishes each for seeds from feces of *Alouatta palliata mexicana*, *A. pigra*, *Cercopithecus aethiops*, and *Pongo pygmaeus*; eight dishes with seeds from feces of *Pan troglodytes*; and five dishes with seeds from feces of *Papio hamadryas*. There were fewer dishes for chimpanzees and baboons because the high fiber and indigestible material in their fecal samples made it difficult to obtain more seeds. All dishes were placed in a thermostatically controlled chamber, for 16 hr at 27°C (without light) and 8 hr at 30°C (with light) [Serio-Silva and Rico-Gray, 2002]. The seeds were checked daily for 30 days to verify germination (first appearance of the radicle), and distilled water was added to maintain humidity. For each dish we recorded the germination percentage at the end of the trial and T₅₀ (time needed for 50% of seeds to germinate). We used one-way analyses of variance (ANOVAs) and Tukey tests to analyze differences among treatments in germination percentages (the data were arcsin-transformed) and in T₅₀ [Zar, 1996].

The seed germination percentage differed among treatments (F = 8.41, df = 6, P < 0.00001) (Table 1). Germination was highest for seed defecated by New World monkeys (78%). Seeds from feces of Old World monkeys and apes germinated relatively less (66.6% and 50.5%, respectively), while control seeds exhibited the lowest germination (36%). In particular, seeds defecated by *A. palliata*, *A. pigra*, and *C. aethiops* germinated significantly more than control seeds (Tukey, P = 0.0001, P = 0.0008, P = 0.01, respectively; Table 2). *Alouatta palliata* seeds showed the highest percentage of germination, as well as the fastest germination (Fig. 1 and Table 1). The T₅₀ values for *A. palliata* seeds were significantly different from those for *P. troglodytes*, *C. aethiops*, and control seeds (F = 10.61, df = 6, P < 0.0001; Tukey, P = 0.0003, P = 0.0001, P = 0.0001, respectively).

The seed passage time (Table 1) for apes (*P. troglodytes* and *P. pygmaeus*) was within the range estimated by Milton [1984]. While there are no data in the literature (at least to our knowledge) regarding passage times for *P. hamadryas* and *A. pigra*,

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	PIG	CER	PAP	PON	PAN	Control
PAL PIG CER PAP PON PAN	0.62	0.17 0.98	0.23 0.95 0.99	0.0034* 0.25 0.74 0.96	0.0003* 0.0336* 0.20 0.59 0.94	0.0001* 0.0008* 0.0103* 0.12 0.34 0.95

TABLE 2. Results of Tukey test (ANOVA, F = 8.41, df = 6, P < 0.00001) on germination percentage of fig seeds from feces of six primate species and from syconia (control)[†]

[†]*P*-values refer to multiple comparisons between treatments.

*Significant differences (P < 0.05).

PAL, Alouatta palliata; PIG, Alouatta pigra; CER, Cercopithecus aethiops; PAP, Papio hamadryas; PON, Pongo pygmaeus; PAN, Pan troglodytes.

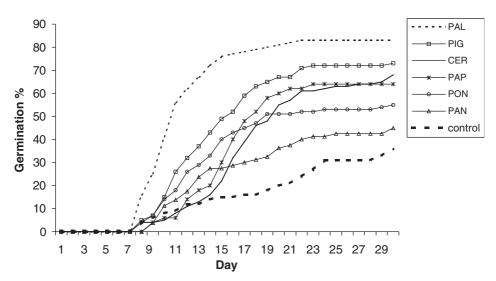


Fig. 1. Germination curves of seeds from feces of the six species of primates, and control seeds. The accumulated germination percentage is plotted vs. time. PAL, *Alouatta palliata*; PIG, *Alouatta pigra*; CER, *Cercopithecus aethiops*; PAP, *Papio hamadryas*; PON, *Pongo pygmaeus*; PAN, *Pan troglodytes*.

the existing data for *C. aethiops* indicate a quite longer food passage rate of approximately 30 hr [Lambert, 1998; Milton, 1998]. However, the mean gut passage time can vary greatly depending on the type and size of ingested seeds, and the amount of food consumed [Traveset, 1998]. Many seeds recovered from the feces of *P. hamadryas* and *P. troglodytes* were not intact, probably because they had been damaged by gastric acids and/or by friction with accidentally ingested small stones (these seeds were not used in germination trials, because they lacked the embryo). In general, different degrees of seed coat scarification are caused by different retention times and chemical or mechanical abrasion [Traveset et al., 2001].

Our results show that seeds from the howlers' feces germinated the most, compared to the rest of the primate species used in this study. Howler monkeys have a capacious colon (43 cm long, 3.5 cm wide) [Milton, 1981] in which food can be

retained for some time (after it passes through the caecum) and fermentation activities can occur. Their hindgut capacity and relatively slow food passage rate appear to be related to an efficient digestion strategy, which can increase seed coat removal and consequently trigger germination. This hypothesis is supported by the fairly high germination rate in seeds ingested by C. aethiops, a primate with similar colon surface area [Chivers and Hladik, 1980] and food passage rate. Even though Cercopithecus monkeys are considered mainly seed predators [Rowell and Mitchell, 1991], fig seeds are so small (<2 mm) that they are generally swallowed and found intact in the feces [Lambert, 1999]. This study confirms that the treatment undergone by fig seeds in the gut of vervets can have a positive effect. However, seeds ingested by A. palliata and C. aethiops differed in speed of germination, with the latter exhibiting a slower germination. In general, rapid germination can be advantageous in the field, because it reduces seed predation [Stevenson et al., 2002]. However, to assess the possible role of primates as seed dispersers, many other factors should be considered, such as the quantity of removed seeds and the sites in which they are deposited.

The results obtained so far reveal some differences in germination among different primate species, and confirm the important role of primates in seed germination success. The differences can be related to the different morphological features of the gut in these species, as well as to other factors that affect food-processing efficiency. However, seed retention time alone can not explain the results of the germination trials, since differences in germination can also be attributed to the chemical composition of food ingested with the seeds [Traveset et al., 2001].

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