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# The Role of Canopy Ants in Removing *Ficus perforata* Seeds from Howler Monkey (*Alouatta palliata mexicana*) Feces at Los Tuxtlas, México[1]


## ABSTRACT

We analyzed *Ficus perforata* seed removal by canopy ants under four treatments: syconia seeds; howler monkey-defecated washed seeds; syconia seeds with howler dung; and defecated seeds with howler dung. Ants removed more defecated washed seeds in the wet season, while during the dry season, removal was greater for syconia seeds and defecated washed seeds. Our results suggest that ants tended to remove more seeds when they were not embedded in feces; however, even seeds set on howler dung were still attractive to ants.



## RESUMEN

Determinamos la preferencia de hormigas para remover semillas de *Ficus perforata* bajo cuatro tratamientos: semillas provenientes de siconos y semillas defecadas por monos aulladores; y dentro de cada uno de estos tipos se colocaron semillas sobre heces frescas. Las hormigas removieron más semillas defecadas en la estación húmeda, mientras que en la estación seca la mayor remoción fue para las semillas de siconos y semillas defecadas. Los resultados sugieren que las hormigas remueven más semillas cuando no están embebidas en excretas, sin embargo también las semillas colocadas en excretas fueron atractivas para las hormigas.


*Key words:* *ants; canopy; deposition sites; defecated seeds;* Ficus perforata*; howler monkeys; Los Tuxtlas; seed removal; tropical rain forest.*

Seed dispersal by animals can either be primary, when animals consume, throw, or remove seeds from the parent plant, or secondary, when vectors remove seeds from where they were primarily deposited (Garber & Lambert 1998). Primates may disperse seeds via their feces (Lambert 2002). In particular, howler monkeys (*Alouatta palliata*) consume large amounts of figs (*Ficus* spp., Moraceae; Shanahan *et al.* 2001), which are considered keystone species for many frugivores (Bleher *et al.* 2003), and disperse their seeds (Serio-Silva & Rico-Gray 2002). Seeds are defecated undamaged by howlers (Stevenson *et al.* 2002), and insects may provide secondary dispersal while removing seeds from fecal clumps (Andresen 2002).

Ants play an important role as seed dispersers in tropical ecosystems (Davidson & Epstein 1989) and their role as secondary dispersal agents has been demonstrated (Passos & Oliveira 2003). Due to these secondary movements, ant-dispersed seeds benefit because seed shadows are altered, seed competition can be avoided (Byrne & Levey 1993), and they have a chance to find a better site for germination and establishment (Kaspari 1993; Passos & Oliveira 2002, 2003). Ants can remove fig seeds from fruits under the parent tree (Roberts & Heithaus 1986), or from feces, redistributing the deposited seeds (Laman 1996). They may also remove seeds defecated by monkeys (Pizo & Oliveira 1999), which may lie on the ground, branches, or leaves. Ants are one of the main canopy-dweller insects (Wilson 1987). Most studies, however, have been done at ground level, and thus little is known about their role as seed dispersers in the canopy. Moreover, because studies on seed removal from howler dung have focused mainly on dung beetles (Estrada *et al.* 1999, Andresen 2001), the role of canopy ants in seed removal and dispersal remains unclear. Interactions between howler monkeys and *Ficus* trees can be important in the regeneration dynamics of tropical forests (Terborgh 1986), and in this study we investigated the effect of canopy ants removing fig seeds defecated by mantled howler monkeys (*Alouatta palliata mexicana*). Because ants can remove seeds either from fruits or vertebrate feces, and foraging activity of ants may vary among seasons (Vogt *et al.* 2003), we addressed the following questions: (1) Do ants in the canopy layer prefer removing seeds from *Ficus* syconia or from howler monkey feces?;(2) Do different seasons influence seed removal pattern?; and (3) Where are the deposition sites following seed removal?

Fieldwork was carried out in a fragment (40 ha) of tropical rain forest in Playa Escondida, Los Tuxtlas, Veracruz, Mexico (18°36′N, 95°05′W). This warm and humid region is characterized by mean

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annual temperatures of 24 to 26°C (max 36°C, min 18°C) and total annual precipitation of 3000 to 4000 mm (Soto & Gama 1997). Although annual precipitation is high, there is a mild dry season from March to May (Estrada & Coates-Estrada 1984).

In March 1999, we followed a troop of howler monkeys for several days while they were foraging on a crop of *Ficus perforata*. Ripe syconia and feces were collected a day after the monkeys fed in a *F. perforata* tree. Syconia and feces were dried and stored until seed extraction. Only seeds of *F. perforata* were present in feces. Seeds were extracted directly from smashed dried figs and from washed feces under a microscope and only undamaged seeds (*i.e.*, containing the embryo) were selected and stored. Only fresh howler monkey feces was used in the seed-removal experiments. In order to get just the fecal material to be used in the seed treatments, we manually removed the seeds from recently collected feces (hereafter referred to as "cleaned feces"). Experiments were carried out four times during the rainy season and four times in the dry season.

Ten wooden platforms (15 x 15 cm) were randomly placed on branches (>5 m above the ground) on each of four *Diospyros digyna* (Ebenaceae) trees, which were used during both seasons. This tree species was selected because it is a typical host for several epiphytes (Serio-Silva & Rico Gray 2002). Seeds represented by all four treatments were placed on 9 cm diameter filter paper in each of the platforms: (1) syconia seeds; (2) defecated washed seeds; (3) syconia seeds set on top of a small pile of cleaned feces (2 cm diam); and (4) defecated seeds set on top of a pile of cleaned feces (2 cm diam). Each treatment in every filter paper had ten seeds during both seasons. Filter paper was placed on the platforms, which was then covered to avoid seeds being washed by rain or removed by animals, but allowed the entrance of ants. Platforms were protected from the direct effect of the rain by a section of triplay, which was separated 1 cm from the box allowing access to ants. We did not observe beetles on monkey feces either before or during the experiment.

The number of ant-removed seeds per treatment per tree was recorded daily, three times a day during five days per experimental session during both seasons. To analyze the proportions of seeds removed per treatment per season, we used a two-way repeated measures ANOVA on two factors (factors: seasons, treatments; subjects: four trees; SigmaStat 1995). Data were arcsine transformed (Zar 1999). Seeds were removed by workers of *Azteca* sp. (Dolichoderinae), *Tetramorium* sp. (Myrmicinae), *Pheidole* sp. 1, and *Pheidole* sp. 2 (Myrmicinae) and although done nonsystematically, defecated washed seeds were offered to these species in order to identify deposition sites. By following loaded ants ($N = 49$), deposition sites were identified as cracks in bark, ant gardens, and ant tunnel-like nests.

We found a significant difference in seed removal between seasons ($F = 11.95$, df = 1, $P = 0.041$), with the highest removal in the wet season. Among treatments, increased numbers of seeds were removed from defecated washed seeds in the rainy season, and from syconia seeds and defecated washed seeds during the dry season ($F = 14.89$, df = 3, $P < 0.001$; Fig. 1). Interaction between factors did not have a significant effect ($F = 1.88$, df = 3, $P = 0.20$).

We studied a part of a complex and little understood interaction involving a two-phase seed dispersal system (Passos & Oliveira 2002). Our results showed that canopy-dwelling ants affect the fate of both defecated and non-defecated fig seeds. *Ficus perforata* seeds lack an elaiosome, but their dispersal is not limited since ants perform both seed dispersal and secondary seed removal, as has been reported for other plant species (Roberts & Heithaus 1986, Passos & Oliveira 2002). Seed removal was higher in the rainy season, and it is possible that relatively lower temperatures favor ant activity, allowing the seeds to be redistributed more often than during other periods of the year when seed removal rates may decrease. Defecated seeds represent a strong attractant for many insects (Andresen 2001) because as feces fall to the ground (hitting branches or leaves), their odor is easily detected. Our results showed that defecated washed seeds were removed in higher proportions by ants, suggesting that they may still maintain feces' odor (Kaufmann *et al.* 1991). Seeds from syconia were also removed, and their sugary, viscous coat (Ramirez 1977) has been suggested to be an ant reward. The embryo itself represents a food source (Sallabanks & Courtney 1992), and even though predation occurs, seeds may escape because ants accidentally drop seeds while carrying them to the nest (Laman 1996).

Seeds set on feces had lower removal, possibly because feces began to get solid after a couple of days and seeds were trapped, suggesting that seeds without feces were more accessible to ants. It is crucial that dispersed seeds reach a proper microsite for germination and establishment (Chambers & MacMahon 1994). In this study, *Azteca* transported seeds to tunnel-like nests ($N = 26$). *Pheidole* sp.1 ($N = 1$) and

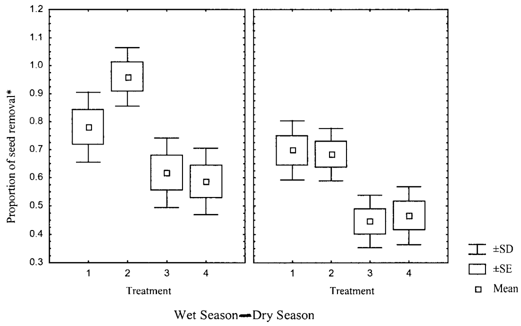


FIGURE 1. Proportion of seed removal by ants in four treatments during wet and dry seasons. Treatment (1) syconia seeds; (2) defecated washed seeds; (3) syconia seeds set on top of a pile of cleaned feces; and (4) defecated seeds set on top of a pile of cleaned feces.

* Arcsine transformed data.

*Tetramorium* sp. workers carried seeds into cracks in the bark ($N = 20$). During our sampling time, we did not observe any seeds germinating or any seedlings on our sampled trees ($x = 4$); however, several months later (during a trip to Playa Escondida) when fieldwork had been accomplished, we did find an established 10 cm long *Ficus* seedling on one of the sampled trees. The seedling was located inside a crack in the bark on the canopy. Such moist sites are rich in organic material (Longino 1986) and may favor germination of *Ficus* (*Urostigma;* Ramirez 1977, Kaufmann *et al.* 1991). Moreover, monkey feces were found as part of the structure of *Azteca* nests, suggesting that ants may use vertebrate feces to enrich their nests and to obtain salt supplements (Davidson 1988). Feces itself represents a rich environment for seed germination (Chambers & MacMahon 1994). *Pheidole* sp. 2 ($N = 2$) was found carrying seeds to an ant garden, which is rich in organic material and debris (Blüthgen *et al.* 2001) and represents an ideal substrate for seed germination (Longino 1986).

We consider ants as seed dispersal agents (and not seed predators) in this example because they do not use seed parts or break seeds into pieces. They use seeds as a whole and not as seed parts; however, even though seed removal is not a measure of seed dispersal success, it is the first step in the process of dispersal in which seeds can be eaten by the ants but can also escape predation when deposited ("accidentally") in adequate microsites. Due to the latter, we consider ants as participants in the dispersal process more so than as only seed predators. Our results suggest that ants are agents of directed dispersal. The ant nests found during this research had characteristics that were as beneficial for seed germination and seedling establishment (*e.g.,* amount of organic matter and soil humidity); however, some seeds could accidentally be deposited outside the nest, and thus, we would need to quantify the number of seeds reaching the nest relative to the seeds deposited outside the nest. Also, although the benefits that ants may provide as post-dispersers are difficult to quantify and detect (Sallabanks & Courtney 1992; *cf.* Passos & Oliveira 2002), this study showed that they may play an important role by removing seeds from different sources. Trials on seed germination and seedling survival after ant post-dispersal processes in the canopy are necessary to better evaluate this system.

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