

## The Impact of Seed Harvesting Ants (*Pheidole* sp. nov.) on *Ficus* Establishment in the Canopy<sup>1</sup>

*Key words:* ants; *Ficus*; hemiepiphyte, Indonesia; *Pheidole*; secondary seed dispersal; seed predation.

A RECURRING QUESTION ABOUT THE BIOLOGY of hemiepiphytic *Ficus* trees has been what limits their establishment success on host trees, and thus ultimately, their population density in tropical forests (Janzen 1979, Putz & Holbrook 1986, Michaloud & Michaloud-Pelletier 1987). The great tropical botanist Corner (1940) was perhaps the first to raise this question, writing: "Considering how vigorous they are and how easily their seeds are distributed, it is a problem why strangling figs do not occur on most big trees in the forest. In parks and 'padangs' that are little cared for, they are generally common, occurring on every tree which is the roosting place for birds. Possibly ants carry off and eat many of the fig seeds."

Despite Corner's early conjecture, little is known about the potential effect seed harvesting ants in the canopy may have on hemiepiphytes. Reviews of the biology of hemiepiphytic *Ficus* have made no reference to canopy ants (Janzen 1979, Putz & Holbrook 1986). Ants, however, are prominent components of canopy fauna (Erwin 1983, Wilson 1987), and ant-epiphyte mutualisms have been well-studied (Davidson 1988, Davidson & Epstein 1989, Davidson & McKey 1993). Ants are also well-documented in various interactions with plants in terrestrial systems (Buckley 1982, Beattie 1985, Hölldobler & Wilson 1990, Levey & Byrne 1993), including seed predation and secondary dispersal of fig seeds in Costa Rica (Roberts & Heithaus 1986). The observation that seeds of several strangler fig species are transported by *Crematogaster* ants to carton-covered runways in tree crevices in Peru (Davidson & Epstein 1989), hints at possible interaction of ants and hemiepiphytic *Ficus* in the canopy. Secondary seed dispersal by terrestrial ants of the introduced hemiepiphyte *F. microcarpa* in Florida also suggests that canopy ants may be attracted to seeds of this species in its native forests of Asia (Kaufmann *et al.* 1991).

Here I report on *Ficus* seed harvesting by an undescribed species of arboreal ant in the genus *Pheidole* discovered in the Bornean rain forest canopy. I consider how seed predation and possible secondary dispersal by canopy ants could ultimately affect hemiepiphyte reproductive success.

This research was conducted at the Cabang Panti Research Site in Gunung Palung National Park, West Kalimantan, Indonesia (1°13'S, 110°7'E) in primary lowland mixed dipterocarp forest less than 100 m above sea level. The average annual rainfall of 4300 mm is relatively evenly distributed throughout the year with typically one drier month with less than 100 mm of rain between June and September.

This study was part of a broader ecological study of factors affecting *Ficus* seedling establishment in the canopy, focusing on the large hemiepiphytic fig *Ficus stupenda* Miq. which predominantly colonizes trees in the Dipterocarpaceae (Laman 1994). Forty-five mature dipterocarp trees representing ten species from the genera *Shorea* and *Dipterocarpus* were selected for climbing and used as a base for canopy experiments and observations. Five of the selected trees contained adult *F. stupenda* individuals, while the remaining 40 were free of large hemiepiphytic figs. In addition to these criteria, trees were selected because of their suitability for climbing and for conducting other canopy experiments. I was unaware of the existence of *Pheidole* sp. nov. at the time of tree selection. Trees were climbed using "single rope technique" and modifications thereof (Perry 1978, Nadkarni 1988, Dial 1994, Laman 1995a). The 45 study trees were each climbed multiple times, ranging from four to over ten times each.

Ants in the genus *Pheidole* were collected and observed repeatedly in 9 of the 45 trees surveyed. In addition, ants believed to be members of the same species were observed, but not collected, in two other trees. Eleven of 45 (24%) trees thus contained *Pheidole*. Stefan Cover (Museum of Comparative Zoology, Harvard University) made the taxonomic determination that all specimens represent a single undescribed species, which I refer to as *Pheidole* sp. nov. Voucher specimens are deposited in the Museum of Comparative Zoology. Like all members of the genus *Pheidole*, this species has two castes: large soldiers (head widths  $1.69 \pm 0.08$  mm; mean  $\pm$  SD,  $N = 6$ ), and much smaller workers (head widths  $0.68 \pm 0.02$

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TABLE 1. *Distribution of young Ficus seedlings encountered in the canopy in relation to the presence or absence of Pheidole sp. nov. in trees.*

	Number of trees with <i>Ficus</i> seedlings	Seedlings per tree		Total seedlings
		Mean $\pm$ SD <sup>a</sup>	Range	
<i>Pheidole</i> sp. nov. present	3	3.3 $\pm$ 1.5	2-5	10
<i>Pheidole</i> sp. nov. absent	12	20 $\pm$ 31.0	1-106	239

<sup>a</sup> Difference between groups not significant (Mann-Whitney *U*-test,  $P > 0.05$ ).

mm; mean  $\pm$  SD,  $N = 6$ ). Soldiers were never observed patrolling the tree and were only seen when recruitment to a large food source occurred. During the course of all canopy work, opportunistic observations were also made on other ant species.

*Pheidole* colonies were located by placing baits of granulated sugar on several branches or sites in the crowns of trees and following ants back to nest sites. *Pheidole* were successfully followed to their nest locations in four trees. One nest was in a tree crotch beneath the epiphyte mat, two were among epiphytes in the crevices between a hemiepiphyte and host trunk, and one was in a rotting branch stump. In no instances were seeds transported down the trunk of the tree. Thus I suspect that this species is strictly arboreal.

A canopy fig seed planting experiment was conducted in which groups of 20 *F. stupenda* seeds were planted in each of 336 canopy microsites distributed among the 45 study trees (Laman, 1995b). The seeds used in this experiment had been recently extracted from freshly fallen figs, washed thoroughly in water, and air dried, and were thus free of any other fruit parts. *F. stupenda* seeds lack any attached food body (elaiosome) such as that reported for *F. microcarpa* (Kaufmann *et al.* 1991), but do have a viscid water-absorbing coating. During the course of this experiment, *Pheidole* sp. nov. were observed on repeated occasions to collect *F. stupenda* seeds that were placed on tree surfaces and transport them back to presumed nest sites. When groups of twenty fig seeds were placed in one site, workers often encountered the seeds within minutes, each carrying away one seed. Other workers were often quickly recruited to the site. In the year-long experiment following the fate of seeds planted in the canopy, the presence of *Pheidole* sp. nov. on a tree had a highly significant negative effect on fig seed germination and seedling establishment success (Laman, 1995b).

In addition to the experimental fig seed plantings, all naturally occurring *Ficus* seedlings in the canopy were also documented in the 45 study trees. A total of 249 young *Ficus* seedlings at the two to four leaf stage were encountered in the canopy and utilized for a comparison of seedling abundance in trees with and without *Pheidole*. The distribution of wild *Ficus* seedlings showed a pattern of negative association with trees containing *Pheidole* (Table 1). The mean number of seedlings found on trees without ants was much greater than on *Pheidole* trees. However, there was no statistically significant difference between groups because of large variation in seedlings per tree. Although three of the *Pheidole* ant trees had *F. stupenda* adults that fruited during the study, producing high seed input into their own crowns, the result was only a few seedlings on two of the trees. In contrast, one of the *F. stupenda* without *Pheidole* also fruited and produced 106 seedlings on its surface. These patterns support the idea that *Pheidole* ants are potent *Ficus* seed harvesters in the canopy that limit the recruitment of fig seedlings.

To examine why *Pheidole* sp. nov. were present on some trees and not others, data were collected on factors that might affect tree canopies as ant habitats. The total epiphyte load on each tree was characterized by estimating the percent of the upper bole and upper branch surfaces that were covered by epiphytes to the nearest ten percent. "Epiphyte load" was loosely defined to include trunk and branch-climbing lianas as well as epiphytes, in order to obtain a measure of surface cover on the tree. The presence or absence of each of the following classes of canopy plants was noted for each tree crown: *F. stupenda* hemiepiphytes; *F. punctata* Thunb. (an ivy-like trunk climber in the subgenus *Ficus* section *Kalosyce*); other lianas that occupied area on the trunk or main branches; ferns; orchids; mosses; and the large epiphytic screw-pine *Pandanus epiphyticus*. Possible associations between ants and all canopy plant groups were examined with chi-square tests of independence.

TABLE 2. Association of *Pheidole* sp. nov. with classes of canopy plants in a survey of 45 canopy trees in the family Dipterocarpaceae greater than 70 cm DBH. *Pheidole* sp. nov. was found in 11 of the 45 trees.

Canopy plant category	Occurrence of plant type		Number expected with ants	Number Observed with ants	$\chi^2$	P
	N	%				
<i>Ficus stupenda</i> hemiepiphyte	5	11	1.2	3	3.85	0.05
<i>Ficus punctata</i> trunk climber	18	40	4.4	8	6.50	0.01
Other trunk zone lianas	36	84	9.3	10	0.46	0.50 NS
Ferns	21	47	5.1	6	0.36	0.55 NS
Orchids	31	69	7.6	8	0.10	0.75 NS
Mosses	31	69	7.6	6	1.40	0.24 NS
<i>Pandanus epiphyticus</i>	10	22	2.4	2	0.14	0.71 NS

*Pheidole* were most frequently observed in the dipterocarps with *F. stupenda* hemiepiphytes. Although the sample of five *F. stupenda* trees examined is small, three out of five of these *F. stupenda* trees had *Pheidole* ants (60%), compared with 20 percent of trees without *F. stupenda* that had ants (Table 2). *Pheidole* nest sites were readily located in each of the three *F. stupenda* with *Pheidole*. *Pheidole* ants were also found to be significantly associated with the presence of the trunk-climbing species of fig, *Ficus punctata* (Table 2). Ant presence was not associated with any of the other canopy plant classes examined (Table 2). Tree DBH and overall epiphyte load showed no significant differences between the "ant" and "no ant" groups (Mann-Whitney U-test, NS). *Pheidole* were found on five different dipterocarp species in the study. The distribution of ants in relation to tree species was tested, but there was no significant association of *Pheidole* ants with particular dipterocarp species ( $\chi^2 = 3.87$ ,  $df = 3$ ,  $P = 0.28$  NS). However, given the limited sample sizes of each tree species (ranging from 5–14), this test had limited power to detect any patterns.

The observations reported here suggest that arboreal *Pheidole* could be potent seed predators that limit *Ficus* reproduction. No *Ficus* seedlings were found in the vicinity of *Pheidole* nests, suggesting that the ants are consuming the seeds, not simply eating the viscid coat and discarding the seed. This interpretation is also in keeping with the seed eating habits typical of this genus (Perry & Fleming 1980, Hölldobler & Wilson 1990). Nonetheless, ants may drop seeds in transport, or discard or abandon them in or around nest sites, and the possibility of *Pheidole* sp. nov. acting as secondary seed dispersers must also be considered.

From the plant's perspective, the important question about interactions that combine seed predation and secondary dispersal is whether the overall benefit to the plant's fitness is enhanced or reduced. Even if an ant that mostly consumes seeds provides some degree of secondary dispersal to quality sites, unless the net result is superior overall seed dispersal compared to what the plant would experience without the ant, it is an antagonistic relationship. Thus the key question is how many quality safe sites would have been hit without the ant (or other seed predator/disperser), as opposed to how many were hit with the ant's involvement? The outcome could be related in a complex fashion to the density of seed rain into safe sites and the efficiency of the ants. Consider a hypothetical canopy tree with five good fig establishment sites in crotches or knotholes. One of these is occupied by an ant colony. If seed rain is dense, then all five sites may be hit by seeds, but if ants collect all seeds and only deposit some at the nest site, then the outcome for the plant is a reduction in seed dispersal quality. If seed rain is light, on the other hand, and none of the five good sites are hit by seeds, but ants collect seeds from other places on the tree and deposit some at their nest site, then the plant would experience enhanced dispersal quality. I hypothesize that relative effects of seed predator/dispersers on a plant's fitness could vary across the landscape in relation to the density of safe sites and the level of seed rain. Further work will be required to understand these complex interactions.

What might account for the positive association between the presence of *Ficus* adults and ants in the same trees? Occupying the same tree as a hemiepiphyte such as *Ficus stupenda* that produces large fig crops would provide access to seeds in fig fragments and vertebrate feces that landed on branches. Ants thus could preferentially colonize fig trees, survive better in fig trees, or forage frequently in fig trees

because of the food source. Alternatively, suitable ant nest sites may be a limiting resource in the canopy (E. O. Wilson, pers. comm.), and trees with hemiepiphytes on them may contain many suitable nest sites (such as the crevices between tree and strangler roots). This seems especially likely in the case of the climbing fig *F. punctata*, which produces only small numbers of figs but entwines the host trunk extensively.

Titus *et al.* (1990) have noted that fig seedlings are rarely found growing on conspecifics. *Pheidole* sp. nov. appear to have a predilection for occupying fig trees and reduced the numbers of seedlings on *F. stupenda* adults in this study. If seed harvesting ants are preferentially occupying fig trees and collecting their seeds in the canopy, then ants could be one of the factors contributing to a low frequency of fig seedling establishment on conspecifics.

*Pheidole* sp. nov. was the only ant species observed to collect seeds experimentally placed in the canopy. On two occasions in the canopy of trees not included in this study, numerous individuals of *Polyrhachis* sp. were observed harvesting fig seeds from civet feces. On one occasion they transported clumps of fig seeds in fecal material across a large liana to another tree before descending to the ground, while on the other occasion they carried seeds into a nest in a large tree crotch. In both cases many fig seeds were dropped by the ants at various points along their routes, and some were discarded on refuse piles around the nest in the second case. *Polyrhachis* sp., though less common than *Pheidole* sp. nov. in the trees surveyed, is an example of another ant species that could also impact hemiepiphyte reproduction in the canopy.

Previous discussions of factors that may be limiting the establishment of *Ficus* hemiepiphytes on rain forest trees have not considered the possibility of ants in the canopy as a contributing factor (Janzen 1979, Putz & Holbrook 1986, Michaloud & Michaloud-Pelletier 1987). However, surveys of ants from other locales also suggest that seed harvesting ants may be important in the canopy. For example, the Tambopata ant fauna analyzed by Wilson (1987) included nine species in the genus *Pheidole*, and in a survey in New Guinea Wilson (1959) also reported *Pheidole* ants living in the canopy, finding many seeds stored in their nests. The results presented here suggest that Corner's early insight may have been correct (Corner 1940). Arboreal ants deserve further consideration as we try to understand the ecology of hemiepiphyte reproduction.

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