Growth and survival of incipient ant colonies in two Amazonian ant-plants: Effects of habitat, host-plant, and mode of colony founding (Hymenoptera: Formicidae)

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Heraldo Vasconcelos
Universidade Federal de Uberlândia (UFU)

Growth and Survival of Incipient Ant Colonies in Two Amazonian Ant-plants: Effects of Habitat, Host-plant, and Mode of Colony Founding (Hymenoptera: Formicidae)

by

A.S. Nery[1] & H.L. Vasconcelos[2]

ABSTRACT

We assessed the effects of habitat type, host-plant species, and mode of colony founding on the survivorship and growth of incipient colonies of ants (Hymenoptera: Formicidae) associated with two Amazonian ant-plants. We experimentally colonized seedlings of *Maieta guianensis* with founding queens of *Crematogaster laevis* or *Pheidole minutula*, and of *Tococa bullifera* with *Azteca* sp., *C. laevis*, or *P. minutula* queens. Seedlings were then transplanted to two habitats: stream edges or forest interior, where they remained for 75 days. To prevent subsequent, natural ant colonizations we caged plants with a fine mesh. Overall, levels of mortality were greater for small bodied queens of *P. minutula* (50-75%), than for larger bodied queens of *C. laevis* (38.7-53.6%) and *Azteca* sp. (12.5-25.0%). While seedlings grew faster along stream edges, in general, habitat type did not significantly affect colony survival and growth. The exception to this trend was observed for colonies of *P. minutula*, which survived better in seedlings located on stream edges. We found a trend of greater survival of *C. laevis* in *T. bullifera* than in *M. guianensis*, but no effect on colony growth. In contrast, the performance of *P. minutula* in *T. bullifera* was very poor, probably because *T. bullifera* is not a usual host of *P. minutula*. Mode of colony founding did not affect survival of *P. minutula* colonies in *M. guianensis*. However, pleometrotic colonies (with 5 queens) grew significantly faster than single queen colonies, and at a rate comparable to colonies of *C. laevis*. This suggests that pleometrosis can be a beneficial strategy, at least when levels of intra- and inter-specific competition among incipient colonies is high.

Keywords: Ant-plant interactions, colony founding, myrmecophytes, pleometrosis, tropical forests

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[1] Programa de Pós-Graduação em Entomologia, INPA, CP 478, 69011-970 Manaus, AM, BRAZIL. Email: andrea.nery@uol.com.br

[2] Corresponding author: Instituto de Biologia, Universidade Federal de Uberlândia, CP 593, 38400-902 Uberlândia, MG, BRAZIL. Email: heraldo@umuarama.ufu.br

INTRODUCTION

Myrmecophytes, or ant-plants, produce special structures of primary or secondary origin -known as domatia-, where ants nest (Benson 1985). The colonization by founding queens of ant species associated with myrmecophytes generally occurs early in plant development. At this stage, several incipient colonies of the same or different species can be found in different domatia of the same plant, but later only one colony will succeed and dominates the entire plant (McKey 1984; Verhaagh 1994; Maschwitz & Fiala 1995; Dejean & Djieto-Lordon 1996; Yu & Davidson 1997; Federle *et al.* 1998). Mortality of founding queens and incipient colonies can be high (McKey 1984; Yu & Davidson 1997), and this probably results from the combined effects of competitive displacements by conspecific and non-conspecific colonies, chance events, predation, parasitism and pathogen attacks (McKey 1988). The incidence and magnitude of at least some of these factors can vary according to the habitat where the host-plant is growing. For instance, in Peruvian *Cecropia*, attack of founding queens by parasitoid wasps is intense in riverside plants, but weak to absent in the patchily distributed forest gap plants (Yu & Davidson 1997). Habitat conditions, especially light, can also affect rates of resource (food and nesting space) supply to ants (Davidson & Fisher 1991; Folgarait & Davidson 1994), and thus indirectly affect the survival and growth of the associated ant colonies.

Another important determinant of survival and growth in incipient colonies is the mode of colony founding. Some ant species cooperate to each other at the founding stage, a behavior known as pleometrosis. Empirical studies have show that pleometrosis lowers the mortality rates of founding queens in some species (Waloff 1957; Bartz & Hölldobler 1982), but not in others (Tschinkel & Howard 1983). In addition, pleometrosis can increase the rate of colony growth (Bartz & Hölldobler 1982; Tschinkel & Howard 1983). Pleometrosis has been detected in at least some populations of *Pheidole minutula* (Vasconcelos 1993), a species associated with several Amazonian melastome ant-plants. It has been suggested that pleometrosis could be advantageous for *P. minutula*, since it competes intra- and inter-specifically for host-plants (Vasconcelos 1993).

Here we studied colony founding by ant species associated to two Amazonian ant-plants, *Maieta guianensis* and *Tococa bullifera* (Melastomataceae), that produce leaf pouches as domatia. We compared survival of founding queens and growth of incipient colonies in two forest habitats, stream edges and forest interior, since previous studies have demonstrated that both plant density and identity of the ant associate vary according to habitat type (Vasconcelos & Davidson 2000). The effects of host-plant species and mode of colony founding on colony survival and growth were also examined.

MATERIALS AND METHODS

The study took place between May and November 2000 in a forest reserve situated ca. 70 km north of Manaus (2°25'S, 59°48'W), in Brazilian Amazonia. The reserve is on moderately rugged terrain, dissected by small creeks, and lies at an elevation of 50-100 m. Canopy height of forest trees is about 35 m. The understory is relatively open and characterized by an abundance of stemless palms. Precipitation in Manaus averages 2100 mm annually and varies seasonally, with a rainy period between November and May and a dry period between June and October (Ribeiro 1976).

Seedlings of *M. guianensis* and *T. bullifera* were grown in a shade house until they had produced at least one fully developed domatia-bearing leaf. These seedlings were then experimentally colonized with founding queens, which were obtained by non-destructively opening the domatia of field seedlings (as described in Vasconcelos 1993). If a founding queen was present (including those that eventually had already produced eggs and larvae, but not adult workers) it was removed from the domatium and transferred temporarily to a test tube containing water trapped at the bottom with a cotton plug. Any queen that suffered some kind of injury during the collecting process was eliminated. While our experimental procedure probably caused some stress on queens, which might lead to post-transplanting mortality, our primary objective was not to determine exact rates of mortality but rather to compare mortality across ant species, host-species, and habitats. In this sense, queens subjected to different treatments were manipulated in exactly the same way.

Seedlings of *M. guianensis* were colonized with queens of *Crematogaster laevis* or *Pheidole minutula*, species that naturally colonize this ant-plant (Vasconcelos & Davidson 2000). Since queens of *P. minutula* can present pleometrotic behavior (Vasconcelos 1993), seedlings of *M. guianensis* were colonized with either one or five queens. In total, 59 seedlings were colonized with a single queen, and 60 seedlings with 5 queens each (all queens in the same domatium).

Seedlings of *T. bullifera* were also colonized with queens of its naturally associated species, *C. laevis* and *Azteca* sp. (Vasconcelos & Davidson 2000). However, in addition, we attempted to colonize seedlings with *P. minutula*, which was never found in *T. bullifera*. In the latter case, five cooperating queens were used per seedling. Sixty-three *Tococa* *seedlings were colonized with C. laevis queens, 23 with P. minutula (5 queens per seedling), and 16 with Azteca sp. queens. The low number of seedlings with Azteca sp. reflects the fact that founding queens of this species were relatively rare in our study area.*

Experimental colonization of seedlings took place by transferring one queen from the test tube to the upper surface of the youngest domatia-bearing leaf. This is the leaf most frequently colonized by founding queens (Vasconcelos 1993). Seedlings were then monitored until the queen had entered into the leaf pouch. Colonized seedlings were transferred to the field in the following day. About half of the 283 experimentally colonized seedlings were placed along the edges of a small stream that crossed the reserve, whereas the other half in the interior of the forest, in more shaded conditions. To prevent further colonizations, seedlings were placed inside small cages covered with a fine mesh (1 mm in mesh size). A plate, filled with water, was placed beneath each potted plant, in order to prevent possible terrestrial invaders such as foraging ants.

Seedlings remained in the field for 75 days. At the end of this period, we determined the number of domatia-bearing leaves produced per seedling, the number of queens alive, and the number of eggs, larvae, pupae, and workers produced per colony.

Statistical analyses

We used a test for comparing two proportions for data in the form of a 2 x 2 contingency table (Zar 1984, pp. 395), in order to assess eventual differences in survival between ant species, or within ant species as a function of host-plant species or habitat. This is a more powerful test than the Chi-square test. However, the power of the test depends on sample size (Zar 1984). Therefore, in some cases, our hypothesis tests were conservative. This was the case with *Azteca* sp., with which we were able to colonize only a relatively small number of seedlings.

Differences in growth of incipient colonies were assessed using Analysis of Variance. The dependent variable, number of workers and pupae produced in 75 days, was log transformed prior to the analysis in order to meet the assumptions of data normality. Independent variables were ant species, or host-species, and habitat.

Differences in growth of seedlings transplanted to different forest habitats were assessed using t-tests. We calculated relative growth rates as (Nf – Ni)/Ni, where Nf is the number of domatia-bearing leaves at the end of the experiment, and Ni is the initial number of domatia-bearing leaves.

RESULTS

Plant growth

Seedlings of *M. guianensis* transplanted to stream edges grew faster than those transplanted to forest interiors (Relative growth rates: stream edges = 0.60 ± 0.06 (S.E.), forest interiors = 0.15 ± 0.04; t = 5.897, df = 178, $p < 0.001$). Most (70%) of the stream edge plants produced at least one new domatia-bearing leaf over the course of the experiment, whereas few (26.7%) of those in the forest interior produced domatia. Seedlings of *T. bullifera* also tended to grow faster along stream edges (Relative growth rates: stream edges = 0.31 + 0.08 (S.E.), forest interiors = 0.14 + 0.10), but the difference was not significant (t = 1.376, df = 82, p = 0.173).

Mortality of colonizing queens

We considered a queen as dead when we found its corpse or body parts, either in the plant or outside, on the soil surface or in the plate placed beneath each potted seedling. Missing queens were not included in the analysis of mortality, although it is likely that these also represented events of true mortality, as missing queens occurred more frequently in situations were we detected more mortality (Table 1).

Table 1. Fate of founding queens of *Pheidole minutula*, *Crematogaster laevis*, and *Azteca* sp. in different host-plants or habitats.

Host-Plant	Ant	Habitat	Initial no. queens, or group of queens	Situation after 75 days Number missing	 Number dead	 % mortality*
Maieta	*Pheidole* (1 queen)	Stream edges	29	6	13	56.5
		Forest interior	30	6	18	75.0
	Pheidole (5 queens)	Stream edges	31	1	15	50.0
		Forest interior	29	6	17	73.9
	Crematogaster	Stream edges	30	0	15	50.0
		Forest interior	31	3	15	53.6
Tococa	*Crematogaster*	Stream edges	34	3	12	38.7
		Forest interior	32	1	11	35.5
	Azteca	Stream edges	8	0	1	12.5
		Forest interior	8	0	2	25.0
	Pheidole (5 queens)	Stream edges	10	7	0	n.d.**
		Forest interior	11	9	2	n.d.

* Excluding missing
** Not determined given small sample sizes

Mode of colony founding was not an important determinant of survival in colonies of *P. minutula*. Haplometrotic (1 queeen) and pleometrotic (5 queens) colonies presented comparable levels of mortality ($Z = 0.577$, $p = 0.282$; Table 1). Therefore, for the subsequent analysis we combined data from both colony types.

For all ant species there was a trend towards greater mortality for queens established in forest interior seedlings than for those in stream edge seedlings (Table 1). However, for *Azteca* sp. and *C. laevis*, habitat differences in mortality were relatively small. For *P. minutula*, in contrast, mortality was 40% greater in forest interior seedlings than in stream edges (74.5 versus 52.8%, $Z = 2.24$, $p = 0.013$).

When comparing different ant species in the same host-plant species, we found that in *M. guianensis* mortality was greater for *P. minutula* than for *C. laevis* (63.0 versus 51.7%, $Z = 2.03$, $p = 0.021$). In *T. bullifera*, we found a trend of greater mortality for *C. laevis* than for *Azteca* sp (37.1 versus 18.8%), although not statistically significant given small sample sizes ($Z = 1.39$, $p = 0.083$).

Survival of *C. laevis* tended to be greater in *T. bullifera* than in *M. guianensis* (37.1 versus 51.7%; $Z = 1.61$, $p = 0.053$). By contrast, performance of *P. minutula* in *T. bullifera* seedlings was very poor. Only 3 out of 21 colonies were alive at the end of the experiment (Table 1). Most (76.2%) were missing, which suggests that either they died at the very beginning of the experiment, or that they abandoned the plant.

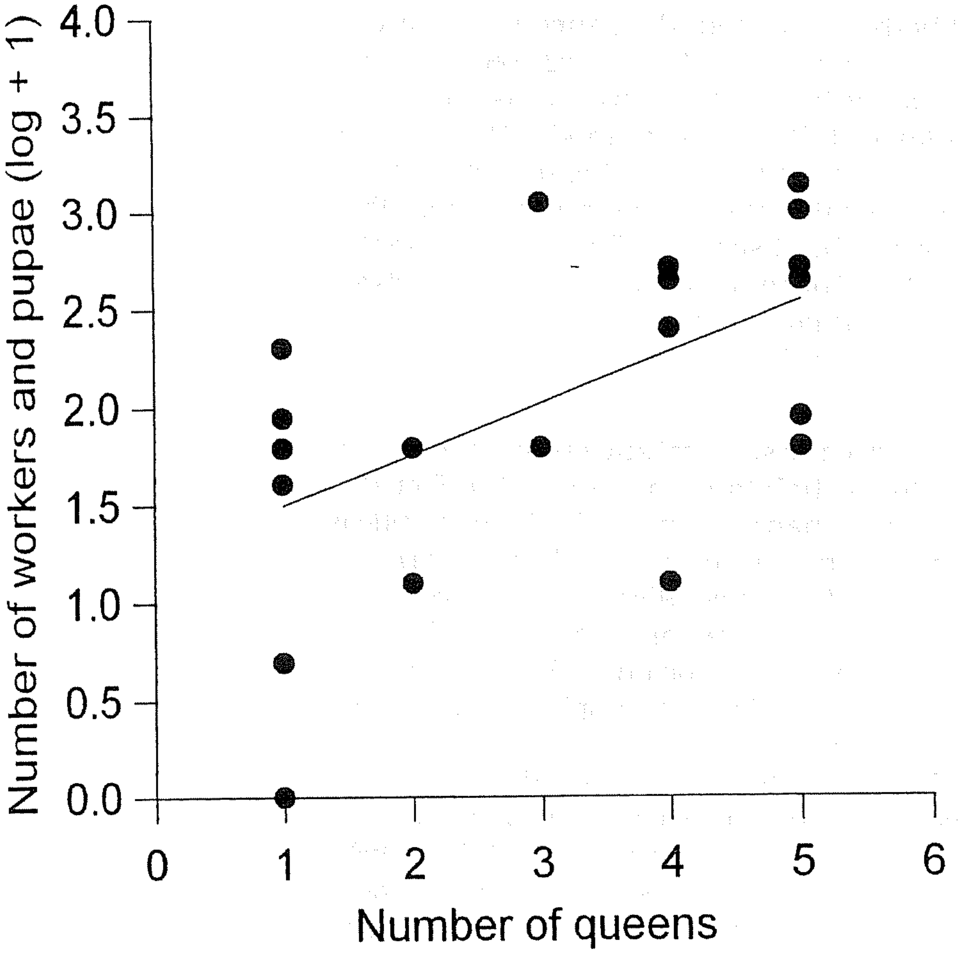
Growth of the incipient colonies

There were differences both within- (regarding mode of colony founding) and between-species in relation to the growth rate of incipient colonies established in *M. guianensis* (Table 2). Haplometrotic *P. minutula* colonies grew slower than pleometrotic colonies. In addition, *P. minutula* colonies founded by a single queen grew slower than those of *C. laevis* (also founded by a single queen), whereas colonies founded with five queens grew at the same rate as those of *C. laevis* ($F_{2,59} = 8.89$, $p < 0.001$, Table 2). Overall, there was no significant effect of habitat ($F_{1,59} = 1.31$, $p = 0.23$), with incipient colonies of all species growing as fast in *M. guianensis* transplanted to stream edges as in those transplanted to the forest interior.

Part of the variation in colony growth of the pleometrotic *P. minutula* colonies was explained by variations in the number of queens alive at the end of the experiment. There was a positive and significant relationship between the number of queens alive after 75 days and the number of workers and pupae produced during the same period ($F_{1,19} = 8.06$, $p = 0.01$; Fig. 1).

ble 2. Number of eggs, larvae, pupae and workers produced by founding queens of *Pheidole inutula*, *Crematogaster laevis*, and *Azteca* sp. over a 75 day period. Values represent the mean 1 S.E.

ost-Plant	Ant Inhabitant	No. eggs	No. larvae	No. workers & pupae	*N*
Maieta	*Pheidole* (1 queen)	3.2 ± 1.1	0.6 ± 0.3	1.2 + 0.4	16
	Pheidole (5 queens)	6.6 ± 1.6	8.9 + 3.7	8.8 ± 1.4	21
	Crematogaster	4.2 ± 0.9	2.2 ± 0.4	7.5 ± 2.0	28
Tococa	*Crematogaster*	8.1 ± 1.7	4.4 ± 0.9	8.7 ± 1.5	38
	Azteca	5.5 ± 1.3	3.8 ± 0.9	9.4 ± 3.2	13



ig. 1. Relationship between the number of cooperating queens of *P. minutula* alive after 75 days Q) and the number of workers and pupae (W) produced during the same period in seedlings of he ant-plant *M. guianensis* (Log W + 1 = 1.24 + 0.26Q, r^2 = 0.298).

In *T. bullifera*, we did not detect any difference in growth between *Azteca* sp. and *C. laevis* ($F_{1,47}$ = 0.02, p = 0.99), and here again no habitat differences in colony growth was found ($F_{1,47}$ = 0.43, p = 0.61). Comparative analysis of the growth of *C. laevis* colonies in different host species indicated that they grow equally well in *M. guianensis* as in *T. bullifera* ($F_{1,62}$ = 0.17, p = 0.68; Table 2).

DISCUSSION

Interspecific differences in mortality

Colony founding by *Azteca* sp., *C. laevis*, and *P. minutula* is fully claustral, as we never saw queens of these species leaving the domatium to forage. Both *Maieta* and *Tococa* produce small leaf emergences, described as glandular trichomes or food bodies, on their abaxial leaves and inside domatia (Roth 1976, Svoma & Morawetz 1992). There is evidence that these trichomes serve as food for the ant larvae (Roth 1976, Svoma & Morawetz 1992). Whether or not founding queens also feed on glandular trichomes is not clear. If not, then, their energy requirements to produce eggs and raise the larvae have to be derived, as is the general case of ants founding colonies in fully claustral mode (Hölldobler & Wilson 1990), from the histolysis of the thoracic wing muscles and fat bodies. Differences in body size, and therefore in food reserves, may thus have accounted at least in part for the observed differences in mortality between the three species studied. Queens of *Azteca* sp. and *C. laevis* are much bigger than those of *P. minutula*, and the latter suffered greater mortality than the former at the founding stage.

Habitat effects

Overall, little difference existed in the survival and growth of incipient colonies located in different forest habitats, in spite of the fact that seedlings grew faster in stream edges than in the more shaded condititions of the forest interior. This suggests that, in contrast to the pattern found for expanding and mature colonies (Fonseca 1999), plant growth is not an important determinant of success in incipient colonies. The only species whose colony performance varied according to habitat type was *P. minutula*, which survived better in plants transplanted to stream edges. However, it is unlikely that this is due to differences in rates of food supply (glandular trichomes) between stream edge and forest interior seedlings, as otherwise differences in colony development would also have been detected and this was not the case. More likely, differences in mortality were due to differences in rates of pathogen attack, since other external sources of mortality, such as predators and parasitoids, were excluded by caging plants with a cloth mesh. Signs of fungal attack were found in many dead queens of *P. minutula*, although we were not able to determine whether these were in fact pathogens or simply saprophytic fungi.

Effects of host-plant species

For *C. laevis* we found a trend, although only marginally significant, of greater survival of founding queens in *T. bullifera* than in *M. guianensis*, a result which is consistent with the fact that mature colonies of *C. laevis* are more common in the former than in the latter (Vasconcelos & Davidson 2000). More detailed studies are necessary to confirm this trend and determine the reasons for the differential mortality. One possibility includes the fact that the domatia of *T. bullifera* are larger than those of *M. guianensis*. This suggests that *T. bullifera* provides more food to their associated ants. However, here again, eventual differences in food supply did not translate into differences in colony growth, since *C. laevis* grew as fast in *T. bullifera* as in *M. guianensis*. Another possibility is that the larger internal space of *T. bullifera* domatia allows greater ventilation, and this may reduce rates of fungal infection on *C. laevis* queens, comparatively to *M. guianensis*.

Performance of *P. minutula* queens in seedlings of *T. bullifera* was very poor. Very few survived and in most cases we did not find corpses or body parts in the plant, which suggests that many founding queens died soon after colonization or, most likely, tried to abandon the plant. If so, selection of host-species by founding queens, and not post-colonization events, is probably the factor accounting for the absence of mature *P. minutula* colonies in *T. bullifera* (Vasconcelos & Davidson 2000).

Pleometrosis in *Pheidole minutula*

Conforming to some other studies on pleometrotic ants (e.g., Tschinkel & Howard 1983) we have found that, in *P. minutula*, although pleometrosis does not lowers mortality rates of founding queens, it increases colony growth relative to single queen colonies (Table 2). The observed relationship between the number of queens alive and the number of workers produced in pleometrotic colonies (Fig. 1), suggests that the greater the number of founding queens the greater the rate of colony growth. What remains to be determined is whether or not this relationship is unimodal, since in other species studied the production of workers reaches a maximum with a certain number of founding queens and then declines (e.g., Bartz & Hölldobler 1982, Tschinkel & Howard 1983). In *P. minutula*, the average number of founding queens per colony is 2.7, with no more than 11 queens being found in the same domatium (Vasconcelos 1993). This latter figure is probably determined by physical space, since, obviously, there is a maximum number of queens that can fit into a given domatium.

One of the most likely advantages of pleometrosis in *P. minutula* is at competitive contests for domination of the host-plant. In *M. guianensis*, subsequent colonizations of the same individual by different ant species (*P. minutula* or *C. laevis*) occur usually within a month (Vasconcelos 1993). Queens of *C. laevis* are much bigger than those of *P. minutula* (one order of magnitude difference in body weight), and therefore are probably able to dislodge existing *P. minutula* queens. However, this trend can probably be reversed by the presence of a small worker force, and in this respect pleometrotic colonies are able to build one faster than single queen colonies. The faster growth of pleometrotic colonies can be also advantageous when multiple queen colonies compete with single queen colonies, since in ants the outcome of territorial contests is frequently determined by asymmetries in colony size (Adams 1990).

CONCLUSIONS

Overall, our results suggest that resources provided by the host-plant have little or no influence on the establishment success of incipient plant-ant colonies. This is evidenced by a general lack of effect of habitat on colony survival and/or growth. Habitat effects on colony survival existed only for *P. minutula*, but in this case it is likely that the effect was mediated by differences in rates of pathogen attack on founding queens rather than by differences in rates of resource supply by host-plants. It is clear, however, that resource supply by host-plants will affect colony performance at later stages in colony ontogeny (i.e., at the ergonomic and reproductive stages, sensu Hölldobler & Wilson, 1990), since in plant-ants colony size is affected by host-plant size and condition (Janzen 1975, Fonseca 1999). At the founding stage, colony success seems to be determined not only by chance events, predation, and competition, but also, as indicated here, by idiosyncrasies of the species, such as queen size and mode of colony founding.

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