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The Biology of Leaf Nesting Ants in a Tropical Wet Forest¹

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ABSTRACT

The nest and colony characteristics, distribution, and ecology of four taxonomically diverse species of ants that build nests on leaf surfaces in a tropical wet forest are documented and compared. Significant differences were observed in the material used to construct nests, in the nest architecture, nest and colony size, social organization, nest density and distribution, and in the apparent food habits of the four species. The observed differences between the four species reflect the great taxonomic distance between them and indicate that each evolved the leaf nesting habit independently rather than through a common leaf nesting ancestor. The leaf nesting habit does not put obvious, common constraints on the nest or colony characteristics or the ecology of ant species, but may limit ants of this lifestyle to habitats and microsites that have a narrow range in ambient temperature and relative humidity.

NEST BUILDING IS AN ALMOST UNIVERSAL BEHAVIOR IN ANTS. The majority of species build nests (see Wheeler 1910, Sudd 1967 for review) in the soil, but other species nest above ground in crevices (Forel 1874), rotting wood (Riordan 1960, Soulie 1961), the specialized parts of plants (Bequaert 1922, Brown 1960), in carton nests on the sides of trees (Forel 1899, Wheeler 1922), and on leaf surfaces (Forel 1894, Hölldobler & Wilson 1983). Descriptions of the nest and colony characteristics and ecology of ant species that nest on leaf surfaces are infrequent and largely limited to species of the genera *Oecophylla* (Wheeler 1910, Way 1954), and *Polyrachis* (Forel 1928, Hölldobler & Wilson 1983), which make nests by weaving leaves together with silk. Other ant taxa that build carton or fungal nests on leaf surfaces have been reported (Wheeler 1910, Forsyth 1981) and described taxonomically, but very little information is available on the distribution, abundance, social organization, ecology, and evolution of these taxa.

This paper presents information on the nests and colonies of four species of previously unstudied ants that build nests on leaf surfaces in a Costa Rican lowland wet forest. The abundance and distribution of each species within the forest are also described and inferences are made concerning both the ecology of these species and the evolution of the leaf nesting habit in ants.

MATERIALS AND METHODS

This research examined four species of ants that build nests on leaf surfaces: *Apterostigma collare* Emery and *Pheidole fiorii* Emery (Subfamily Myrmicinae), *Tapinoma*

inrectum Forel (Subfamily Dolichoderinae), and *Paratrechina caeciliae* Forel (Subfamily Formicinae). Nests and colonies of the four leaf nesting ant species were examined in both the laboratory and the field at Finca La Selva, a wet forest field station and site of the Organization for Tropical Studies in Heredia Province, Costa Rica. Nine to eleven nests of each species were selected from the primary forest for measurement, collection, and dissection. The nests were chosen to exemplify the wide range of nest and colony sizes; they do not represent a random sample of each species' nests or colonies. The maximum length, width, and height of each nest was recorded in the field. The nests were then collected by clipping the occupied leaf and sealing the nest and leaf in a plastic bag. Following collection the bagged nests were frozen to immobilize the ants, then the ants and brood of each nest were examined, counted, and preserved. Observations on nest material and nest architecture were also recorded, and nest dry weight was determined. Voucher specimens of each species were deposited at the Natural History Museum of Los Angeles County, California and identified by R. Snelling of the museum staff.

Information on the abundance and distribution of leaf nesting ants was obtained by sampling transects in the primary forest. Three 100-m-long permanent transect lines, approximately 1 km apart, were visited in August, September, and December of 1981 and in April of 1982. At these times information was gathered on all the nests of each leaf nesting ant species that were found within 1 m of one side of a transect line. Transects of shorter length (25 m) were sampled in a similar manner in other parts of the forest in May of 1982. Information was gathered in both transect studies on the height of each nest above ground, the dimensions of the nest, the identity of the plant on which the nest was built, the location of the nest on the leaf, and characteristics of the leaf such as the presence or absence of leaf hairs that were detectable by touch.

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TABLE 1. Nest characteristics of four leaf nesting ant species at Finca La Selva.

	<i>Apterostigma collare</i>	<i>Pheidole fiorii</i>	<i>Tapinoma inrectum</i>	<i>Paratrechina caeciliae</i>
Number of nests dissected	9	10	11	10
Typical nest location	underside of leaves; also branches and tree trunks	underside of leaves	underside of leaves	underside of leaves; also may cement two leaves together
Nest material	fungus mycelia	soil and leaf fragments	soil	soil
Architecture	single domed chamber	many layers of chambers	one layer of chambers	one layer of chambers
Nest entrances	usually one	usually one large and many small	many small	many small
Range of nest dry weight (g)	0.02–0.51	1.22–7.87	0.05–0.33	0.21–1.13
Maximum nest dimensions (mm)				
Length	80	230	106	140
Width	38	65	45	55
Height	26	40	9	13
Correlation coefficients				
Dry wt.—length	0.39	0.63 ^a	0.57 ^a	0.61 ^a
Dry wt.—width	0.61 ^a	0.58 ^a	0.47 ^a	0.39
Dry wt.—height	0.33	–0.15	0.28	0.34
Other material in nest	frass detritus	many seeds; insect remains	—	very few seeds

^a Indicates significance at 0.05 level.

RESULTS

NEST AND COLONY CHARACTERISTICS.—Striking differences are evident between nests of the four species studied (summarized in Table 1). The nests of *Apterostigma collare* are white, dome-like structures made of fungus mycelia. These nests are usually found on the undersides of leaves, but also occur on tree trunks, branches, and on woody vines. *Apterostigma collare* nests typically have a single entrance away from the leaf-nest interface and contain a single chamber that is littered with fungi, insect frass, detritus, and brood. The dissected *A. collare* nests were small and variable in shape with maximum nest width the only nest dimension that was a good indicator of dry weight.

Pheidole fiorii colonies make carton nests of soil and leaf fragments on the undersides of leaves. Nests of this species have poorly defined entrances, but usually contain one large entrance with many smaller ones. *Pheidole fiorii* nests consist of several layers, each of which contains many chambers. Much larger in size than nests of the other three leaf nesting species, dissected nests of *Pb. fiorii* were somewhat rectangular in shape, and dry weight was significantly correlated with both maximum nest length and width. Insect remains and, more commonly, small seeds of several plant families were found in this species' nests; some seeds germinated and grew to be seedlings of a few centimeters while still in the nest.

Tapinoma inrectum builds nests of soil, which are very hard when dry. Located on the undersides of leaves, nests of this species contain many entrances along the leaf-nest interface and on the outer surface away from the leaf. *Tapinoma inrectum* nests are generally rectangular in shape and have little depth with only a single layer of chambers. Nests of this species are small and do not contain obvious stores of food.

The nests of *Paratrechina caeciliae* are made of soil and are usually located on the undersides of leaves, although they can be found cementing two leaves together. *Paratrechina caeciliae* nests are similar to those of *T. inrectum* in that they typically contain a single layer of chambers and have many small entrances, but are often larger than *T. inrectum* nests. The dissected *Pa. caeciliae* nests were variable in shape, but dry weight was significantly correlated with maximum nest length. These nests rarely contain a few small seeds.

There are marked differences among the four species in colony size and social organization (Table 2). *Pheidole fiorii* and *Paratrechina caeciliae* colonies typically contained a single nest, whereas colonies of *Apterostigma collare* commonly occupied more than one nest, and colonies of *Tapinoma inrectum* sometimes contained many nests. Those colonies of *A. collare* which occupied a single nest were small (less than 50 individuals), while single nest

TABLE 2. Colony characteristics of four leaf nesting ant species at Finca La Selva.

	<i>Apterostigma collare</i>	<i>Pheidole fiorii</i>	<i>Tapinoma inrectum</i>	<i>Paratrechina caeciliae</i>
Number of nests per colony	variable but low (1-3)	usually 1	variable; multiple nests common	usually 1
Data on single nest colonies:				
Number examined	6	10	11	9
Range in colony size (# indiv.)	7-52	292-1693	5-295	73-411
Correlation coefficient colony size-nest dry wt.	0.33	0.47	0.51 ^a	0.61 ^a
Range in brood size (# eggs, larvae and pupae)	1-22	155-553	1-174	47-217
Correlation coefficient colony size-brood size	0.13	0.47	0.62 ^a	0.61 ^a
Worker differentiation	monomorphic	polymorphic	monomorphic	monomorphic

^a Indicates significance at 0.05 level.

colonies of the other species were much larger. Single nest *A. collare* colonies also contained the fewest brood with rarely more than 20 brood per nest. In contrast, single nest colonies of *Pb. fiorii* contained as many as 1693 individuals and 553 brood. The number of individuals present in colonies confined to a single nest was significantly correlated with nest size and the number of brood for *T. inrectum* and *Pa. caeciliae*, but no such correlations were observed for comparable *A. collare* and *Pb. fiorii* colonies. Finally, colonies of *A. collare*, *T. inrectum*, and *Pa. cae-*

ciliae are monomorphic and exhibit no morphological differentiation of worker castes, while *Pb. fiorii* colonies are polymorphic and contain a distinct major caste.

NEST DENSITY.—Significant differences were observed in the nest density of these four species within both the permanent transects ($P < .01$) and a series of shorter transects ($P \leq .005$) (Table 3). *Apterostigma collare* nests were most abundant, with *Pheidole fiorii* nests common and *Tapinoma inrectum* nests rare. Although certain leaf

TABLE 3. Nest density (#/100 m²) of leaf nesting ant species along permanent and temporary transects.

Sample date transects	Permanent transects											
	<i>Apterostigma collare</i>			<i>Pheidole fiorii</i>			<i>Tapinoma inrectum</i>			<i>Paratrechina caeciliae</i>		
	E	A	B	E	A	B	E	A	B	E	A	B
August 1981	3	7	1	2	3	1	0	1	0	0	0	0
September 1981	3	3	0	0	0	0	0	0	0	1	3	1
December 1981	1	1	2	2	1	0	1	0	0	1	2	0
April 1982	0	1	1	1	1	0	0	0	0	0	0	0

Nest densities of the four species, lumping samples and transects, were significantly different (Kruskal-Wallis test, $H' = 11.88$, $P \leq 0.01$)

Temporary transects												
<i>Apterostigma collare</i>			<i>Pheidole fiorii</i>			<i>Tapinoma inrectum</i>			<i>Paratrechina caeciliae</i>			
Res.	Far	SoW.	Res.	Far	SoW.	Res.	Far	SoW.	Res.	Far	SoW.	
4	0	8	0	2	0	0	0	0	2	0	2	
4	8	4	0	2	4	0	0	2	2	0	0	
4	6	2	0	2	0	0	0	2	0	0	2	
6	0	0	2	2	0	0	0	2	2	0	0	
2	2	0	6	0	0	0	0	0	0	4	0	
10	0	6	0	0	0	0	0	0	0	0	0	

ANOVA results: F comparing species densities = 13.64 $P \leq 0.005$
 F comparing densities in regions = 0.97 N.S.

TABLE 4. Number and proportion of nests of each leaf nesting ant species observed on plants of certain families during the transect studies.

Plant family	<i>A. collare</i>		<i>Pb. fiorii</i>		<i>T. inrectum</i>		<i>Pa. caeciliae</i>	
	#	%	#	%	#	%	#	%
Araceae	21	36.2	1	4.2	0	0.0	3	18.8
Cyclanthaceae	7	12.1	2	8.3	0	0.0	1	6.2
Palmae	29	50.0	21	87.5	5	100.0	10	62.5
Helioconiaceae	1	1.7	0	0.0	0	0.0	0	0.0
Gramineae	0	0.0	0	0.0	0	0.0	2	12.5

nesting species have multiple nest colonies, the densities presented in Table 3 are largely unaffected by multiple nest colonies and reflect the densities of leaf nesting colonies; multiple nest colonies were infrequently recorded on the transects, and colonies that contained more than one nest usually extended out of the sampling area and did not have more than one nest included in the census. The nest density of each species varied considerably within each area sampled, and there was no evidence of significant variation in nest abundance between the areas sampled ($P \geq .5$).

NEST DISTRIBUTION.—Possible associations between ant species and plant families were investigated (Table 4), and sample sizes were large enough for three ant species to indicate clear patterns of distribution. Nests of *Apterostigma collare*, *Pheidole fiorii*, and *Paratrechina caeciliae* were typically built on plants of just three families, the Araceae, Cyclanthaceae, and Palmae. Palms were the most frequent nest site of all three ant species; within this plant taxa, these ants utilized at least seven genera as nest sites. Extensive qualitative sampling away from the transects produced observations of *A. collare*, *Pb. fiorii*, and *Pa. caeciliae* on plants of other taxa, but such observations were rare relative to the number of nests observed on aroids, cyclanths, and palms. The fourth leaf nesting ant species, *T. inrectum*, was observed nesting along the transects solely upon palms, but this sample size is small, and observations away from the transects indicate that this species also commonly nests on dicotyledonous trees of several families.

Although these ant species utilize similar plant taxa for nest sites, and nests of different species are occasionally observed on the same individual plant, Figure 1 shows the vertical distribution of these species' nests to be significantly different. This finding suggests that these ant species differ both in their spatial utilization of a given host plant and in their proximity to ground based resources and predators. *Apterostigma collare* and *Pheidole fiorii* nests occurred most frequently between 0.5–1.0 m above ground, but were found up to 2.5 m. *Paratrechina caeciliae* nests were rarely encountered below 1 m and were most frequent

between 1.0–2.0 m. *Tapinoma inrectum* nests were not observed below 1 m or higher than 4 m on the transects, but were observed above 15 m off the transects.

These four ant species also differed in the parts of leaves chosen as nest sites. Table 5 summarizes data obtained on the location of nests on leaves. Chi-square analysis comparing the observed nest placement with that expected if nests were randomly located on leaves shows that each leaf nesting species was sensitive to leaf morphology and constructed nests at characteristic, non-random sites on leaves, and also that the species differed greatly in the location of nests on leaves. *Apterostigma collare* typically built nests along the midrib in the basal or middle thirds of leaves, while *Tapinoma inrectum* constructed nests along the midrib in the middle or distal thirds of leaves. *Pheidole fiorii* and *Paratrechina caeciliae* usually placed nests from one margin of the leaf (width-wise) to the other in the distal third of leaves.

Every ant species examined in this study appeared to be sensitive to the presence of hairs on leaf surfaces and nested exclusively on hairless leaves. The examination of over 200 nests both on and off the transects produced only one observation of a nest being constructed on a leaf that had hairs detectable by touch. Because plant taxa that have hairy leaves are common in the forest (such as species of the Melastomataceae), the absence of leaf nesting ants on hairy plants suggests that the ants avoid hairy leaves as nest sites.

DISCUSSION

The present research has documented the nest and colony characteristics, abundance, and distribution of four species of leaf nesting ants in the primary forest at Finca La Selva. These species exhibited marked differences in the material used to build nests, in nest size and architecture, in colony size, and in social organization. Significant differences were also observed in the abundance of these species in the forest and in both their vertical distribution and their placement of nests upon leaves.

Many of the differences apparent in the nests and

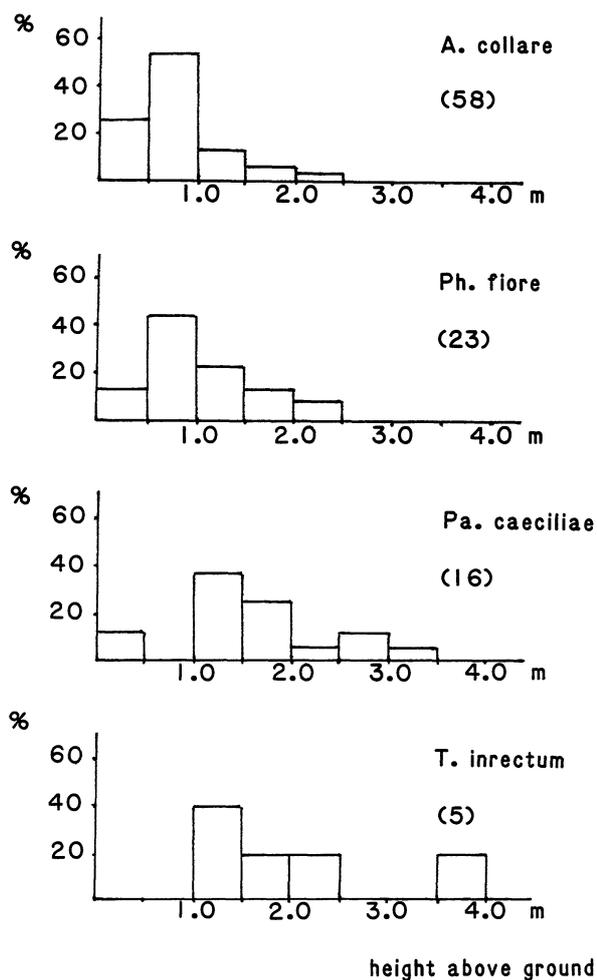


FIGURE 1. Histogram showing percent (%) nests of each leaf nesting ant species found in various height strata. A Kruskal-Wallis test comparing distributions produced an $H' = 41.2$, which indicates significant ($P < .005$) differences in distributions.

colonies of these ant species reflect ecological differences between them. For example, *Apterostigma collare* constructs nests of fungus and utilizes the fungus as its food source, while the other three species make carton nests and have very different foods. *Pheidole fiorii* appears to eat the small seeds that it stores in the chambers and walls of its nest, and *Tapinoma inrectum* and *Paratrechina caeciliae* do not cultivate or cache food within their nests but rely upon food that is produced and ingested entirely outside the nest. Since other species of both *Tapinoma* (Wheeler 1910) and *Paratrechina* tend symbionts (Wilson 1971) and utilize honeydew or nectar as their major food source, it seems likely that *T. inrectum* and *Pa. caeciliae* also utilize honeydew or nectar as a primary food. The

four leaf nesting ant species present at Finca La Selva can thus be separated on the basis of nest material and apparent food habits into three disparate groups with only *T. inrectum* and *Pa. caeciliae* showing possible overlap in utilized food resources.

The four leaf nesting ant species exhibit distinct distributions in the primary forest which further reflect differences in their nests and ecology. Significant differences were observed in the vertical distributions of these species' nests, with *Apterostigma collare* and *Pheidole fiorii* nests found near the forest floor and *Tapinoma inrectum* and *Paratrechina caeciliae* nests observed at greater heights. The proximity of *A. collare* and *Ph. fiorii* nests to the forest floor is probably related to the greater abundance of needed resources on the ground relative to on leaf, stem, or branch surfaces. *Apterostigma collare* must forage for the insect frass and detritus used as substrate for its fungus gardens, and both items are probably much more abundant on the ground and on leaf surfaces near the ground than on leaves and limbs found at greater heights. Similarly, *Ph. fiorii* relies upon small seeds as a primary food and this resource is certainly more abundant on and near the ground than well above the forest floor. In contrast, *T. inrectum* and *Pa. caeciliae* probably tend symbionts or gather nectar on leaves, plant stems, and flowers and certainly do not find greater concentrations of their food resources on or near the ground than in the forest substory.

These four species also exhibit significant differences in the location of nests upon leaf surfaces. The fragile nests of *Apterostigma collare* are usually built along the midrib in the basal third of the host leaf and appear to be well protected from wind and rain in this location. The nests of the other three species are less fragile, but much heavier than are those of *A. collare* and are typically located in more distal regions of the leaf. This is especially true of *Pheidole fiorii* and *Paratrechina caeciliae* nests which often extend from one margin of the host leaf to the other in the distal third of the leaf.

The many differences observed in the biology and ecology of these ant species are not surprising given the taxonomic distance separating them. This four-species array includes species of three subfamilies, the Myrmicinae, Formicinae, and Dolichoderinae, respectively, and includes species on both sides of the two major lines of descent in ants (Wilson *et al.* 1967). These three subfamilies exhibit very distinct specializations, each of which probably evolved under unique selection pressures and with different constraints being placed upon various aspects of their biology and ecology.

In this light, it seems obvious that the leaf nesting habit must have evolved independently for each of these species. The leaf nesting habit is not only uncommon for each of these three ant subfamilies, but it also has not been reported for any of the many other species of these four genera. With both great taxonomic disparity between

TABLE 5. Number and proportion of nests of each leaf nesting ant species found on different areas of leaf blades. χ^2 values presented here were calculated assuming that the nests are placed randomly on leaves and distributed equally in regions of equal area. *Ph. fiorii* and *Pa. caeciliae* nests often extended from one margin of a leaf to the other, and data from these species could not be separated into midrib or margin categories.

	<i>Apterostigma collare</i>		<i>Pheidole fiorii</i>		<i>Tapinoma inrectum</i>		<i>Paratrechina caeciliae</i>	
	#	%	#	%	#	%	#	%
Leaf taken lengthwise								
Basal	28	50.9	0	0.0	1	7.7	0	0.0
Mid	26	47.3	3	12.0	6	46.2	5	25.0
Distal	1	1.8	22	88.0	6	46.2	15	75.0
χ^2	24.2 ^a		34.3 ^a		3.9		17.7 ^a	
Leaf taken widthwise								
Midrib	53	91.4	—	—	13	92.9	—	—
Margin	5	8.6	—	—	1	7.1	—	—
χ^2	39.7 ^a				12.0 ^a			

^a Indicates significance at 0.05 level.

these species and the absence of any similar species that maintain the same leaf nesting habit, the occurrence of a leaf nesting ancestor that is common for the four species examined here seems very unlikely.

The four species examined here are the first species of their respective genera to be reported to have evolved the leaf nesting habit, but show no other major differences in nest and colony characteristics or ecology to other species of each genus. This suggests that the evolutionary transition to nesting on leaf surfaces did not necessitate significant changes in the nests, colonies, or lifestyle of these species. For example, all of the species of *Apterostigma* described to date build small, bag nests out of fungus. These species cultivate the fungus within the nest on a substrate of insect frass and detritus, and utilize the fungus as both a food source and nesting material. The only obvious differences between these species is that *A. collare* builds nests on the undersides of leaves, while other species of this genus nest in more protected areas such as in cavities in rotten wood or underneath large stones. Similarly, *Pheidole fiorii*, *Tapinoma inrectum*, and *Paratrechina caeciliae* are distinct from other species of their respective genera only in that each builds nests on leaf surfaces. The many nest and colony characteristics documented here for these species are well within the range of values shown by other species of each genus, except for the location of their nests; these species are the only species of each genus thus far reported to nest on leaf surfaces.

If the evolution of the leaf nesting habit did not involve major changes in the lifestyle or ecology of these species then why are there not many other species that have also evolved such that they build nests on leaf surfaces? There have been very few reports of non-weaver ants that nest on leaf surfaces (Wheeler 1910, 1922; Forel 1928), and these studies collectively described less than a dozen species. A factor which is important and probably limiting to any

ant species that nests on leaves is the physiological stress caused by fluctuations in the ambient temperature and relative humidity of any ecosystem. The nests of leaf nesting ants provide little insulation, and the ants and brood within the nest are probably subject to the full range of environmental variation that occurs at the nest site. Ants are very sensitive to temperature and relative humidity and extremes of either parameter can cause the death of eggs, larvae, and adults (Wheeler 1922). For example, Vanderplank (1960) examined the reproduction of the leaf nesting weaver ant *Oecophylla* at a range of temperatures and determined that the larvae of this species died at temperatures above 33°C and did not develop at 16°C, but grew to be adults in 18–23 days at 20–30°C. This range of temperatures within which *Oecophylla* larvae can develop is typical of many ant species (Fielde 1905, Wheeler 1910). Species with such requirements for nest temperatures and which nest on leaf surfaces are therefore probably limited to habitats that rarely or never exceed critical temperatures. This certainly seems to be true at Finca La Selva as the four leaf nesting ant species are common only near the ground in the primary forest where temperatures range from 20–25°C. These species are largely absent from the primary forest canopy and from light gaps and successional areas where temperatures are more extreme and frequently range from 15–35°C. Leaf nesting ants are also absent from many other sites in Costa Rica that appear to have abundant leaves of the appropriate taxa for use as nest sites, but which undergo extremes of temperature not observed at Finca La Selva. The apparent paucity of ant species that have evolved the leaf nesting habit thus may be due more to the rarity of habitats that always have temperatures within this critical range than due to other common constraints that the leaf nesting habit puts on the nest and colony characteristics or ecology of any ant species.

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