FORAGER POLYMORPHISM AND FORAGING ECOLOGY IN THE LEAF-CUTTING ANT, *ATTA COLOMBICA*

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ABSTRACT

I compare forager size and foraging selectivity of the leaf-cutting ant *Atta colombica* and that of its close relative *Atta cephalotes*. In both species, larger foragers cut fragments of greater mass and area, and at vegetation sources of greater specific density (mass/area). However, the size-range of *A. colombica* foragers (1.5–56.8 mg) was wider than the range typical for *A. cephalotes* (1.4–32.1 mg). In *A. colombica*, the maxima workers (24–60 mg) commonly participate in foraging, making up 13% of all foragers in this study and in a previous study. In contrast, *A. cephalotes* maxima workers (24–100 mg) rarely forage (less than 1% of all foragers in two previous studies), but instead serve primarily as soldiers defending the nest. Thus, *A. colombica* maxima workers are smaller and do not appear to be so specialized as soldiers as are *A. cephalotes* maxima workers. The broader size-range of workers participating in foraging appears to allow *A. colombica* to exploit a wider range of resources than *A. cephalotes*, including tougher, denser vegetation and fallen fruits.

INTRODUCTION

Leaf-cutting ants of the genus *Atta* are the most important agricultural pests of the New World tropics (Wilson, 1986). Three species of *Atta* occur in Central America: *Atta sexdens* (L.), *Atta colombica* Guérin, and *Atta cephalotes* (L.) (Weber 1972). *A. sexdens* is fairly easy to distinguish from the other two *Atta* species using morphological characters (Weber 1968, 1969; Mackay and

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Mackay, 1986). *A. colombica* and *A. cephalotes*, however, are very similar in appearance and often difficult to distinguish. Emery (1913) considered *A. colombica* to be a subspecies of *A. cephalotes*, saying that the differences between the two taxa were simply related to the degree of polymorphism, with *A. colombica* having soldiers that were smaller than *A. cephalotes* soldiers. Later, however, Emery (1922) separated *A. colombica* and *A. cephalotes* as two distinct species.

Currently, the most reliable morphological character for distinguishing *A. colombica* workers from *A. cephalotes* workers is the luster of their integument: *A. colombica* workers are entirely matte, while *A. cephalotes* workers have shiny areas, particularly on the head and pronotum (Weber 1968, 1969; J. Longino, pers. comm.). Another character often used for distinguishing these two species in the field is that *A. colombica* is the only species of *Atta* reported in the literature to have external refuse dumps for exhausted fungus garden substrate (Haines, 1978). The presence of an external refuse dump indicates that the *A. "cephalotes"* colony studied by Hodgson (1955) in Panama was almost certainly an *A. colombica* colony.

A. colombica is known from Colombia, Panama, Costa Rica, and Guatemala, whereas *A. cephalotes* is widespread from Brazil to Mexico (Kempf, 1972; Weber, 1972). Where colonies of these two species of leaf-cutters come into direct contact, prolonged territorial battles may ensue (J. Longino, pers. comm.). Several studies have compared the ecology of *A. colombica* and *A. cephalotes*. Weber (1969) described both *A. colombica* and *A. cephalotes* as "forest or forest-grassland ecotone species," stating that "the ecological relations between *cephalotes* and *colombica* remain to be determined." Several authors found that when the two species occur together in the same area, *A. colombica* tends to be more common in younger forest, with *A. cephalotes* more common in the older forest (Rockwood, 1973; Feener and Moss, 1990; Orr, 1992). Mackay and Mackay (1986) stated that *A. colombica* usually occurs in drier areas, while *A. cephalotes* is found in a diversity of habitats. Rockwood (1973), however, proposed that *A. colombica* occurs in wetter areas than *A. cephalotes*.

The foraging ecology of *A. colombica* and *A. cephalotes* appears to be fairly similar. Mature colonies of both species primarily

attack the leaves of trees, preferring the younger, softer leaves (Shepherd, 1985; Vasconcelos, 1990). My preliminary observations, however, indicate that in *A. colombica* the largest "maxima" workers (24–60 mg) regularly participate in foraging, whereas *A. cephalotes* maxima workers (24–100 mg) seldom forage. In the present study, I examine forager size and foraging selectivity of *A. colombica*, and evaluate ecological similarities and differences between *A. colombica* and *A. cephalotes*.

METHODS

I conducted this study with several large colonies of *Atta colombica* on Barro Colorado Island (BCI), Panama in July 1992. In addition, I considered more informal observations of *A. colombica* that I made on BCI in August 1990.

At the main *A. colombica* study colony (colony A), I collected 25 laden ants from each of three foraging trails in order to evaluate the match between forager mass and vegetation resource types. I selected foraging trails coming from three very different vegetation sources: 1) a tree with thin, soft leaves, 2) a tree with tough, veiny leaves, and 3) a crop of thick fig leaf stipules scattered on the forest floor.

I placed each ant with her load in a separate 2.5 ml vial, and anesthetized the ants by placing the vials in a refrigerator for several minutes. I then measured the mass of each ant (m_A) and each load (m_L) to the nearest 0.1 mg on a Mettler balance. In addition, I measured the area (α) of each leaf and stipule fragment using a Licor area meter.

From mass and area data I calculated the following measures: burden (β) = the ratio of load mass to ant mass (m_L/m_A); individual load specific density (δ) = m_L/α; overall specific density (D) for each vegetation source = the sum of the load masses divided by the sum of the 25 areas.

To normalize distributions, I performed all regression analyses on log-transformed data. I calculated "residual log load mass" values by subtracting the log load mass values predicted by the log ant mass versus log load mass regressions (for the combined data from all 75 ants) from the actual observed log load mass values. I calculated "residual log load area" values in an analogous manner.

At a second *A. colombica* colony (colony B) where foragers along one trail were carrying whole berries and berry fragments, I collected 10 ants laden with whole berries. I did not collect foragers with berry fragments.

At several additional *A. colombica* colonies on BCI, I collected the largest unladen workers I could find (along trails and exiting disturbed nests) in an effort to determine the maximum worker size for this species. I weighed each of these ants and measured their head widths under a dissecting microscope using an ocular micrometer. I also measured head widths of *A. colombica* and *A. cephalotes* specimens in the collection at the Museum of Comparative Zoology (MCZ) at Harvard University. Any specimens in the MCZ collection that appeared to be incorrectly identified I sent to John T. Longino for verification. *A. colombica* voucher specimens from this study have been deposited in the MCZ.

RESULTS

Forager mass and load size

Overall, the *A. colombica* foragers from colony A (n = 75: three collections of 25 ants each) weighed from 1.5 to 56.8 mg, a 38-fold range of mass (Table 1). Ten of the 75 foragers (13%) weighed more than 24 mg (Table 1).

Specific density varied greatly among the three vegetation sources attacked by colony A (Table 1). The fragments harvested from the thin leaf tree had an overall specific density (D) of 0.12 mg/mm^2 (range of specific density for individual fragments, δ = 0.104 to 0.155 mg/mm^2), whereas the fallen fig leaf stipules had an overall specific density of 0.42 mg/mm^2 (range of δ = 0.263 to 0.726 mg/mm^2). The fragments from the tree with tough veiny leaves consisted of 22 leaf fragments and 3 leaf stipule fragments and were variable in specific density (Table 1; overall D = 0.28 mg/mm^2, range of δ for 22 leaf fragments = 0.187 to 0.361 mg/mm^2 and for the 3 stipule fragments = 0.351 to 1.206 mg/mm^2).

Mean forager mass also varied greatly among the three vegetation sources (Table 1), from 4.9 mg at the thin leaf tree to 20.6 mg at the fig leaf stipule source. Mean ant mass correlated positively with specific density (Table 1).

Table 1. *Atta colombica* forager mass at different sources compared with data from earlier studies with *Atta cephalotes*. *A. colombica*: foragers from one colony (colony A) collected coming from three different vegetation sources (thin leaf tree, veiny leaf tree, and fallen fig stipules), from a second colony (colony B) carrying whole berries, and data from Lighton et al. (1987). The data from the veiny leaf tree are further divided into data for ants with leaf fragments and for ants with leaf stipule fragments. Overall specific density (D = total mass/total area), mean and range of ant mass (m_A in mg), coefficient of variation of forager mass (CV = mean/SD), and percent of foragers larger than 24 mg (% > 24). *A. cephalotes*: foraging from two earlier field studies (Wetterer 1990a; 1994). In Wetterer (1990a) collections were made during the day and night along a single trail (n = 400 for each) and coming down a grapefruit tree (n = 150 for each). In Wetterer (1994) collections were made along trails coming down 18 trees (n = 50 for each tree; total n = 900).

Source	n	Density (mg/mm^2)	Forager Mass (mg) mean ± SD	range	CV	% > 24
Atta colombica						
Colony A (total)	75	0.12–0.42	11.0 ± 12.3	1.5 – 56.8	1.11	13
thin leaf tree	25	0.12	4.9 ± 2.6	1.5 – 13.1	0.54	0
veiny leaf tree	25	0.28	7.5 ± 5.2	3.1 – 27.2	0.69	4
leaf	22	0.23	6.1 ± 2.0	3.1 – 11.5	0.33	0
stipule	3	0.48	18.2 ± 9.6	8.1 – 27.2	0.53	33
fig stipule	25	0.42	20.6 ± 16.8	4.3 – 56.8	0.82	36
Colony B: berries	10	–	29.5 ± 13.1	16.8 – 52.7	0.45	40
Lighton et al.	154	–	15.2 ± 7.1	3.6 – 35.6	0.47	13
Atta cephalotes						
Wetterer	2000	0.15 – 0.37	4.2 – 11.1	1.4 – 32.1	0.31 – 0.73	0.4

Combining data from all 75 ants, I found that logarithmic relationships between ant mass (m_A) and load mass (m_L), load area (α), and specific density (δ) were all significantly increasing functions (Fig. 1; log m_L = 0.09 + 1.16 log m_A, R^2 = 0.67, n = 75; P < 0.001; Fig. 2; log α = 1.08 + 0.74 log m_A, R^2 = 0.42, n = 75, P < 0.001; Fig. 3; log δ = –0.99 + 0.42 log m_A, R^2 = 0.36, n = 75, P < 0.001). Larger ants cut fragments of greater mass, area, and density.

Examining each vegetation source separately, there was a significant (P < 0.05) relationship between ant mass and load mass and between ant mass and load area at all three sources (Table 2). There was no significant relationship between specific density and ant mass at the thin leaf tree or the fig stipules (thin leaf: log δ = –0.92 + 0.04 log m_A, R^2 = 0.03, n = 25, P > 0.05; stipules: log δ = –0.38 + 0.01 log m_A, R^2 = 0.00, n = 25, P > 0.05). There was a
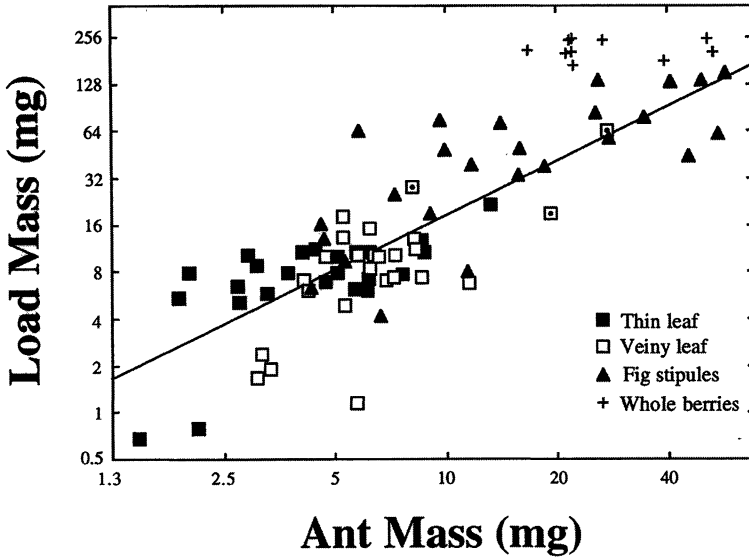
Figure 1. Load mass selection by *Atta colombica* foragers. The logarithmic relationship between ant mass (m_A in mg) and load mass (m_L in mg).The line is the least squares linear regression for the 75 foragers from colony A with vegetation fragments (values for foragers from colony B carrying berries not included in regression calculation). Equation given in text. Closed squares = thin leaf tree; open squares = veiny leaf tree (with dot = leaf stipule); closed triangles = fig stipules; crosses = whole berries.

Table 2. Load size for *Atta colombica* foragers from colony A at three different vegetation sources (thin leaf, veiny leaf, and fig stipule). Burden ($\beta = m_L/m_A$), residual log load mass (log mL), and residual log load area (log α). For each collection, n = 25.

Source	Burden mean ± 1 sd	log m_L regression	R^2	residual log m_L	log α regression	R^2	residual log α
thin leaf	1.8 ± 0.9	0.2 + 0.9 log m_A	0.44	0.002	1.2 + 0.9 log m_A	0.44	0.175
veiny leaf	1.5 ± 0.8	−0.1 + 1.2 log m_A	0.49	−0.125	0.8 + 0.9 log m_A	0.36	−0.170
fig stipule	3.2 ± 2.2	0.5 + 0.9 log m_A	0.55	0.123	0.9 + 0.9 log m_A	0.50	−0.004

significant relationship between specific density and ant mass at the tree with veiny leaves (log δ = −0.87 + 0.33 log m_A, R^2 = 0.17, n = 25, $P < 0.05$), primarily because the three foragers with dense leaf stipule fragments were much larger than the 22 foragers with leaf fragments (Table 1).

Burden ($\beta = m_L/m_A$) ranged from 0.2 to 11.0. Of the three vege-
tation sources, mean burden was lowest at the veiny leaf source
and highest at the fig leaf stipules (Table 2). The load mass cut by
ants of a given size varied among the three vegetation sources; the
mean residual log load mass was lowest at the very thin leaf source
and highest at the stipules (Table 2). The fragment area cut by ants
of a given size also varied among the three sources; the mean
residual log load area was lowest at the veiny leaf source and high-
est at the thin leaf (Table 2). At all three sources, the workers with
loads of the lowest residual area values were among the smallest
workers attacking the source (Fig. 2).

Foragers with whole berries

At *A. colombica* colony B, the 10 foragers that I collected carry-
ing whole berries ranged from 16.8 to 52.7 mg (Table 1). Four of
these foragers weighed more than 24 mg; nine weighed more than
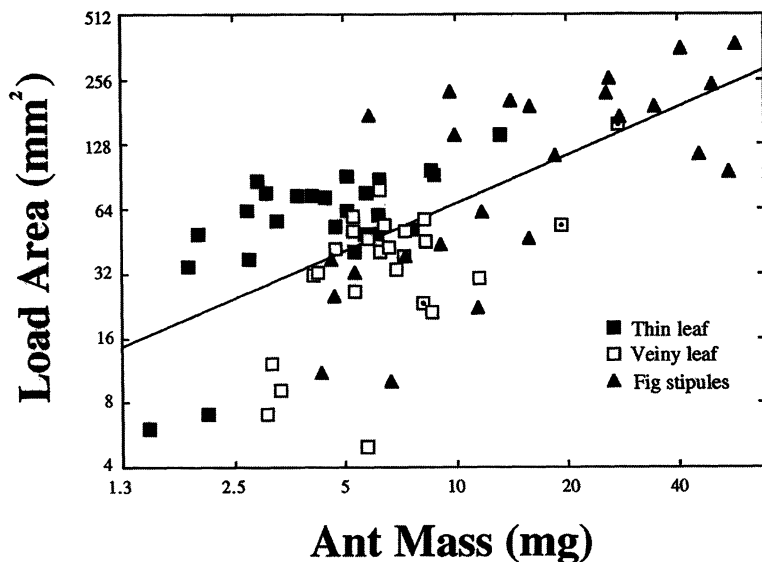20 mg (Fig. 1). The mass of the berries ranged from 177.9 to 247.8

Figure 2. Load area selection by *Atta colombica* foragers. The logarithmic rela-
tionship between ant mass (m_A in mg) and load area (α in mm^2). The line is the
least squares linear regression for the 75 foragers from colony A with vegetation
fragments. Equation given in text. Symbols as in Fig. 1.

mg. Mean burden was 8.3 ± 3.0. Burden ranged from 3.8 for the largest ant to 12.3 for the smallest ant.

The maximum burden of 12.3 is higher than the maximum observed for *A. colombica* foragers carrying vegetation fragments. Foragers appear to be capable of carrying such heavy burdens only when the load is compact like a berry or a flower bud; very large leaf fragments appear to be more difficult to balance (pers. obs.). If the maximum burden possible for *A. colombica* foragers is approximately 12 times body mass, then only workers larger than 14 mg would be able to carry even the smallest of the whole berries. Workers smaller than 14 mg would have to cut fragments from the berries in order to be able to carry the load.

Largest maxima workers

Of the very large unladen *A. colombica* workers I collected from several colonies around BCI, the largest weighed 58.9 mg and had a head width of 4.6 mm. This mass was only slightly greater than the largest laden forager I collected at colony A (56.8 mg). These maximum values are approximately equal to or greater than those previously reported (35 mg - Weber 1968; 60 mg - Lighton et al. 1987; 4.2 mm - Borgmeier 1959). The largest *A. colombica* in the MCZ collection had a head width of 4.2 mm.

The largest *A. cephalotes* worker I have measured weighed approximately 110 mg (Wetterer unpublished) and the largest in the MCZ collection had a head width of 6.4 mm. These maximum values are equal to or greater than those previously reported (103 mg - Weber 1968; 6.1 mm - Stradling 1978; 6.4 mm - Borgmeier 1959).

General observations

I found *A. colombica* on BCI foraging almost exclusively during the day, with very few ants returning to the nest with loads after early evening. All *A. colombica* colonies I observed had external refuse dumps. I found that the ants removed refuse from the nests day and night, as reported by Hodgson (1955).

A. colombica appeared to have foraging trails that were more branching than *A. cephalotes*, simultaneously attacking greater numbers of different vegetation sources. Trails often fanned out through the forest floor to cut crops of fallen leaves, flowers, stipules, sepals, and fruit. I commonly found large *A. colombica* foragers

cutting crops of fallen fig fruits (also see Weber, 1969). This contrasts with Shepherd's (1985) finding of little ground foraging in *A. colombica* in Colombia.

Species identification

Several dozen *A. cephalotes* and *A. colombica* specimens in the ant collection at the Museum of Comparative Zoology (MCZ) at Harvard University were found to be misidentified (pers. obs.; J. Longino, pers. comm.). It seems very likely that some of the published field studies of *A. cephalotes* and *A. colombica* may have also confused the identification of these two species.

DISCUSSION

I found that the size-range of workers participating in foraging was broader for *A. colombica* (1.5–56.8 mg) than for *A. cephalotes* (1.4–32.1 mg; Wetterer 1990a, 1994). Overall, 13% of the *A. colombica* foragers attacking the three vegetation sources weighed 24 mg or more (Table 1). Whether this small sample of vegetation sources is representative of what *A. colombica* foragers generally harvest is unknown. However, Lighton et al. (1987), studying the energetics of *A. colombica* foragers on BCI, similarly found 13% (20/154) of the foragers weighed 24 mg or more (Table 1). In Lighton et al.'s (1987) study, mean forager mass was 15.2 ± 7.1 mg (range 3.6 to 35.6 mg; n = 154). This size-distribution is intermediate for *A. colombica* attacking the two denser vegetation sources in the present study.

In *A. cephalotes*, the largest workers (24–100 mg) rarely forage (Wetterer, 1990a; 1994). Instead, the largest *A. cephalotes* workers appear to function primarily as soldiers, guarding the nest. In two field studies of *A. cephalotes*, I found less than 1% of the foragers weighed more than 24 mg (Table 1; data from Wetterer 1990a, n = 1100; and Wetterer 1994, n = 900). In my 1994 study, the range of densities of 18 trees attacked by *A. cephalotes* was 0.15 to 0.37 mg/mm^2. This appears to be representative of the range of densities of tree leaves typically cut by *A. cephalotes*, though on occasion they attack denser sources, e.g., Rudolph and Loudon (1986) observed *A. cephalotes* attacking the leaves of an epiphyte with a density of 0.58 mg/mm^2. The maxima workers of *A. cephalotes* are larger and appear to be more specialized as soldiers than the maxima

workers of *A. colombica*. Wilson (1984) found a similar trend in species of *Pheidole* where increased specialization of maxima workers was correlated with increased maxima to minima size-ratio, as predicted by caste optimization theory (see Oster and Wilson, 1978).

In both *A. colombica* and *A. cephalotes*, larger foragers cut at denser, tougher vegetation sources and cut the denser, tougher parts of individual sources (Cherrett, 1972; Rudolph and Loudon, 1986; Nichols-Orians and Schultz, 1989; Wetterer 1990b, 1991a, 1994, present study: Table 1, Fig. 3). This match of ant mass to vegetation toughness and specific density appears to increase the efficiency of both cutting (Wilson, 1980) and load delivery (Wetterer, 1994). High specific density and toughness can prevent successful foraging in *A. cephalotes* (Nichols-Orians and Schultz, 1989, 1990). The broader size-range of *A. colombica* foragers may allow them to exploit efficiently a wider range of resources than
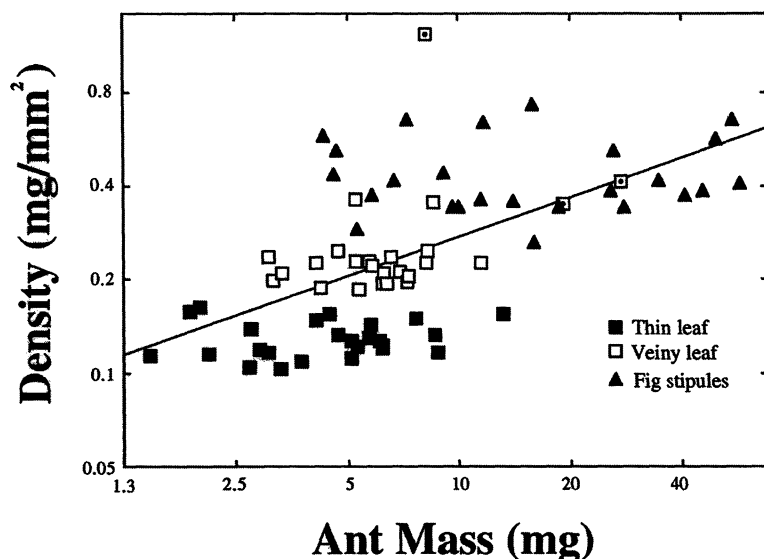

Figure 3. Load density selection by *Atta colombica* foragers. The logarithmic relationship between ant mass (m_A in mg) and load specific density (δ in mg/mm^2). The line is the least squares linear regression for the 75 foragers from colony A with vegetation fragments. Equation given in text. Symbols as in Fig. 1.

A. cephalotes. Indeed, Rockwood (1976) found that *A. colombica* harvested a wider range of plant species than did *A. cephalotes*. The larger foragers of *A. colombica* may allow more successful exploitation of tough resources such as leaf stipules. Large *A. colombica* foragers also may be important in cutting through the thick tough skin of some fruits, such as figs, making the flesh of the fruit available to smaller foragers (pers. obs.).

A. colombica foragers cutting from thick and veiny leaf sources showed a reduction in fragment area cut (Table 2, Fig. 2). *A. cephalotes* foragers show similar reductions under some circumstances, particularly when there is a mismatch between forager size and vegetation source, i.e., when small ants cut very dense vegetation (Wetterer, 1990a; 1994; Roces and Hölldobler, 1994). In *A. cephalotes*, this reduction can be due to many factors including large workers finishing cuts abandoned by smaller workers, large workers taking oversize loads away from smaller workers (Rudolph and Loudon, 1986; Wetterer, 1990a; 1994), and active changes in cutting behavior (Roces and Hölldobler, 1994). In the present study, there is no information as to the mechanism of the reduction.

The maxima foragers of *A. colombica* not only appear to have greater cutting abilities, they also can carry heavier loads (Fig. 1). This can be a particular advantage when harvesting resources such as berries (Table 1, Fig. 1). For possibly similar reasons, *Acromyrmex octospinosus* and *Acromyrmex volcanus*, two species of leaf-cutting ants that depend largely on cutting or collecting fallen fruit, flowers and other vegetation, have very large foragers, large enough to cut or collect any desirable vegetation encountered (Wetterer, 1991b; 1993). In addition to advantages that may result from the use of very large workers as foragers, there are also substantial costs. Larger workers are energetically more expensive to produce than smaller workers, and foragers are generally exposed to greater mortality risks than workers that remain in the nest. Also, parasitic phorid flies preferentially attack larger *Atta* foragers (Orr, 1992), making the maxima foragers particularly vulnerable.

A. colombica and *A. cephalotes* show other ecological differences. On BCI and on the Osa Peninsula in Costa Rica, *A. colombica* are primarily diurnal foragers year-round, whereas *A. cephalotes* forage primarily during the day in the wet season and

primarily during the night in the dry season (Lugo et al., 1973; Feener and Moss, 1990; Orr, 1992). (The observation of diurnal foraging during the dry season suggests that the *A. "cephalotes"* colony studied by Lutz (1929) on BCI may have been actually an *A. colombica* colony.) Rockwood (1975), however, found that although *A. colombica* in Guanacaste, Costa Rica, foraged primarily during the day, they also showed significant foraging at night.

A. cephalotes at La Selva Biological Station in Costa Rica also shift from primarily diurnal foraging in the wet season to primarily nocturnal foraging in the dry season (Wetterer, 1990a). Wetterer (1990a) proposed that this shift could be a mechanism for avoidance of parasitism by diurnal phorid flies that are active in the dry season. At La Selva, however, phorids known to attack *A. cephalotes* appear to be, if anything, more active in the wet season (B. Brown pers. comm.; also see Feener and Brown, 1993). Orr (1992) similarly proposed that avoidance of phorids could explain the differences between the foraging of *A. colombica* and *A. cephalotes* on the Osa Peninsula, because at this site phorids were found only attacking *A. cephalotes*. However, the same pattern of foraging also occurs on BCI, where diurnal phorids heavily attack *A. colombica* foragers (Feener and Moss, 1990).

The phorid flies' differential attack of *A. colombica* and *A. cephalotes* suggests that the pheromones of the two *Atta* species differ. Interestingly, *A. sexdens* may be easily distinguished from *A. colombica* and *A. cephalotes* by the strong lemon-like smell of crushed *A. sexdens* workers (pers. obs.). Brown and Feener (1991) proposed that phorids that use olfactory cues to find their hosts may be important in the evolution of pheromone diversity in ants. What role parasitic phorids might play in the distribution, ecology, and evolution of *A. colombica* and *A. cephalotes* deserves further attention.

A. colombica is the only *Atta* species for which external refuse dumps have been reported in the literature (Haines, 1978). Stefan Cover (pers. comm.), however, has noted such refuse dumps outside *Atta* colonies in Trinidad (the Trinidad species is currently classified as *A. cephalotes*, but may be a separate species, J. Longino pers. comm.; also see Borgmeier, 1950). Fowler (1985) found external refuse dumps in the Paraguayan leaf-cutting ants *Acromyrmex lundi pubescens* and *Acromyrmex landolti*. Neither of

these taxa have any other obvious similarities with *A. colombica*. *Ac. lundi pubescens* is found both in forests and in open habitats and harvests the leaves of dicots, whereas *Ac. landolti* is found only in open habitats and harvests grass (Fowler, 1985). The ecological significance of external refuse dumps remains a mystery (see Haines, 1978; 1983 for further discussion).

Further studies are needed to evaluate the ecological differences between *A. colombica* and *A. cephalotes*. In these studies, it is essential to keep voucher species from each colony under study in order to verify species identification.
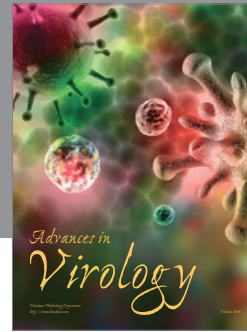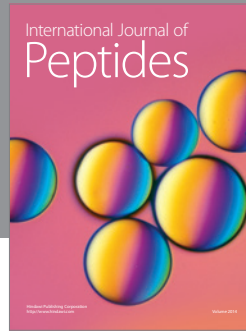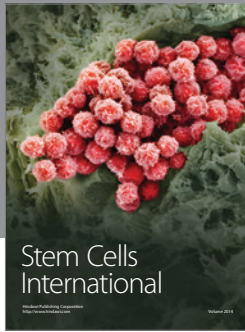
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