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Forager size and ecology of *Acromyrmex coronatus* and other leaf-cutting ants in Costa Rica

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Abstract I compare forager size and foraging ecology of the leaf-cutting ant *Acromyrmex coronatus* (Fabricius) with published data on three other leaf-cutter species in Costa Rica, *Atta cephalotes* (L.), *Acromyrmex octospinosus* (Reich), and *Acromyrmex volcanus* Wheeler. Intra- and interspecific differences in forager size in these leaf-cutting ants appear to reflect the economics of harvesting different preferred resources. *Ac. coronatus* colonies have relatively small foragers (mean mass=3.4±1.4 mg) that cut almost exclusively the thin, soft leaves and other parts of small herbaceous plants. Similarly, small *A. cephalotes* colonies have small foragers (3.3±1.0 mg) that attack the leaves of small herbaceous plants. In contrast, mature *A. cephalotes* colonies have a wider size-range of foragers (7.3±4.1 mg) that primarily attack the leaves of trees, with larger foragers cutting thicker, tougher leaves. In *A. cephalotes*, the match of forager size to leaf type (both ontogenetically and behaviorally) increases foraging efficiency. Extreme forager polymorphism in mature *A. cephalotes* colonies appears to broaden the diversity of tree species that they can exploit efficiently. *Ac. octospinosus* and *Ac. volcanus* both have large, relatively monomorphic foragers (13.3±4.2 mg and 30.6±4.3 mg, respectively) that typically scavenge for pieces of fallen vegetation, such as dead leaves, fruit, and flowers, in addition to cutting herbs. The large foragers of *Ac. octospinosus* and *Ac. volcanus* appear to be well suited as generalist foragers, able to cut or collect any desirable vegetation encountered. *Ac. coronatus* is similar to *A. cephalotes* in other ways. Both *Ac. coronatus* and *A. cephalotes* establish and maintain cleared trunk trails for foraging, and both have minima workers that “hitchhike” on the loads carried by foragers, apparently serving to protect the larger foragers from attack by

phorid flies. Trunk trails and hitchhikers are not known for *Ac. octospinosus* and *Ac. volcanus*. That *A. coronatus* and *A. cephalotes* show little overlap in geographic distribution within Costa Rica may relate both to differences in habitat requirements and to interspecific competition.

Key words *Acromyrmex* · *Atta* · Foraging · Herbivory · Leaf-cutting ants

Introduction

Body size has important implications for many aspects of an animal's biology (see reviews in Peters 1983; Calder 1984; Schmidt-Nielsen 1984; Werner and Gilliam 1984; Reiss 1989). Size-related differences in biology have long been considered central to niche separation (Elton 1927; Hutchinson 1959; but see Simberloff and Boecklen 1981). This is true for both intra- and interspecific differences in size (Peters 1983; Werner and Gilliam 1984). One important aspect of niche that body size can influence is the range of food an animal can exploit efficiently (Elton 1927; Werner and Gilliam 1984; Forsman and Lindell 1993; Benavides et al. 1994; Gordon and Illius 1994; Lindström et al. 1994; Schindler et al. 1994; Werner 1994; Coelho and Hoagland 1995).

Worker size varies intra- and interspecifically among ants (Weber 1972; Hölldobler and Wilson 1990; Wetterer 1994a). If these differences in worker size are shaped by natural selection for economic efficiency, theory predicts that the differences in worker size should relate directly to differences in ecology (Oster and Wilson 1978). For example, Davidson (1977) found that forager size in different species of seed-harvesting ants related to differences in foraging selectivity; species with larger foragers tended to collect larger seeds.

For polymorphic ants, size-related differences are also considered to be central to the economics of division of labor within a colony (Oster and Wilson 1978). Economic theory predicts that “niche differentiation” among

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polymorphic workers, with workers of different size specializing in the tasks at which they are more efficient, should increase the overall efficiency of the colony (Oster and Wilson 1978).

Leaf-cutting ants (Tribe Attini: *Atta* spp. and *Acromyrmex* spp.) are among the most polymorphic of all social insects and show an extensive division of labor among size castes (Wilson 1980a, b, 1983a, b). Foraging is done by medium to large-size workers, who cut and collect plant material which they carry back to the nest. At the nest, smaller workers prepare the retrieved material as a substrate for growing a specialized type of fungus that the ants use for food. One characteristic generally considered to distinguish the two genera of leaf-cutters is that only *Atta* species produce a soldier caste of large workers whose primary function is nest defense (Weber 1972). [For many other divisions of labor, see Fowler and Robinson (1979), Hubbell et al. (1980), and Wilson (1980a)].

Leaf-cutting ants are found only in the New World, ranging from Argentina to Texas. In earlier studies, I examined forager size and foraging ecology in three of the five species of leaf-cutting ants known from Costa Rica: *Atta cephalotes* (L.), *Acromyrmex octospinosus* (Reich), and *Acromyrmex volcanus* Wheeler (Wetterer 1990a, b, 1991a, b, 1993, 1994b, c). I found intra- and interspecific differences in both forager size and foraging ecology. In *A. cephalotes*, forager size and foraging ecology change with colony size (Wetterer 1994c). In small *A. cephalotes* colonies (fewer than 5000 workers), a relatively narrow range of small foragers (mean mass \pm SD=3.3 \pm 1.0 mg) primarily attack the leaves of "herbs," i.e., grasses, ferns, and other small herbaceous plants (97% of all loads; Wetterer 1994c). In large, mature *A. cephalotes* colonies (up to several million workers), a broader size range of workers forage (7.2 \pm 4.1 mg; Wetterer 1994c). In large, mature *A. cephalotes* colonies (up to several million workers), a broader size range of workers forage (7.2 \pm 4.1 mg; Wetterer 1994b), primarily cutting the leaves of large trees in attacks lasting up to several days (Vasconcelos 1990). During these attacks, larger foragers recruit to and cut thicker and tougher leaves (Nichols-Orians and Schultz 1989; Wetterer 1990a, 1994b). In both small and large *A. cephalotes* colonies, minima workers outside the nest generally do not cut vegetation, but rather defend the foragers against attack by parasitic phorid flies, guarding foragers along the trails and on the vegetation, and by "hitchhiking" on loads that foragers carry back to the nest (Feener and Moss 1990).

Compared to *A. cephalotes* foragers, *Ac. octospinosus* and *Ac. volcanus* foragers are much larger (13.3 \pm 4.3 mg and 30.6 \pm 4.3 mg, respectively; Wetterer 1991b, 1993) and relatively monomorphic, with most of the intraspecific variance in forager size due to differences among colonies. *Ac. octospinosus* and *Ac. volcanus* foragers scavenge on fallen leaves, fruits, flowers, and other plant material as well as cut the leaves of herbs (Wetterer 1991b, 1993). *Ac. octospinosus*, and *Ac. volcanus* also differ from *A. cephalotes* in other important ways. *Ac.*

octospinosus and *Ac. volcanus* have much smaller mature colony size (approximately 15000 to 40000 workers; J.K. Wetterer, to be published). Also, in *Ac. octospinosus* and *Ac. volcanus* only the largest workers leave the nest to forage, with no minima workers "hitchhiking" on the loads of others (Wetterer 1991b, 1993).

In the present study, I examined forager size and foraging ecology of a fourth species of leaf-cutting ant in Costa Rica, *Acromyrmex coronatus* (Fabricius). *Ac. coronatus* is common at high elevation sites in Costa Rica, such as Monteverde (elevation 1300–1600 m), but absent from lowland sites, such as La Selva (elevation 40 m). Earlier studies indicated that *Ac. coronatus* differs from *Ac. octospinosus* and *Ac. volcanus* in several ways. For example, *Ac. coronatus* colonies grow considerably larger (150000 or more workers – Pereira-da-Silva et al. 1981) and *Ac. coronatus* minima workers commonly "hitchhike" on incoming loads carried by foragers (D. Feener and B. Brown, personal communication).

Material and methods

I conducted this study in June–August 1993 at three sites on the Atlantic slope of Costa Rica: El Plastico Biological Station (10°18' N, 84°02' W; elevation 560 m), Rara Avis Biological Reserve (10°17' N, 84°03' W; elevation: 700 m), and on the property surrounding at Restaurante La Fonda, Zurquí de Moravia (10°04' N, 84°00' W; elevation: 1600 m). At all three sites, I searched for *Ac. coronatus* foragers and for any indication of *Ac. coronatus* activity. I examined the leaves of plants and trees looking for signs of attack by *Ac. coronatus*: small semicircular cuts from the edges of leaves. *Ac. coronatus* damage could be distinguished from that caused by other leaf-cutting ants because *A. cephalotes* foragers generally cut the entire leaf, including the midvein and *Ac. octospinosus* and *Ac. volcanus* foragers make much larger cuts at the leaf edges. At a fourth site on the Atlantic slope, La Selva Biological Station (10°26' N, 84°00' W; elevation 40 m), I have worked extensively on leaf-cutting ants, but have never found *Ac. coronatus*.

At Rara Avis and Zurquí, I collected laden ants from foraging trails at eight colonies of *Ac. coronatus* located in a variety of habitats (two colonies at Rara Avis: R1 and R2; six colonies at Zurquí: Z1–Z6). Colony R1 was on a forested slope next to a river. Colony R2 was in an open area dominated by live ferns, but surrounded by primary forest. Colonies Z1, Z5, and Z6 were in highly disturbed areas within 10 m of a large highway; colony Z1 in an area dominated by clumps of dead ferns, and colonies Z5 and Z6 in areas dominated by *Gunnera* plants. Colony Z2 was in a somewhat disturbed primary forest area. Colony Z3 was in a mowed grass lawn. Colony Z4 was within a small "island" of trees (about 5 m by 10 m) surrounded by pasture.

At six colonies (R1, R2, Z1, Z2, Z3, and Z4), I placed each ant with her load in a separate 1.7 ml vial. At two colonies (Z5 and Z6), I collected the laden ants in a single 36 ml vial using an aspirator. I anesthetized the ants by placing the vials in a freezer for several minutes. I then measured the mass of each ant (m_A) and each load (m_L) to the nearest 0.001 mg on a Mettler balance. I calculated burden (B) as m_L/m_A .

As in my studies of foraging by *Ac. octospinosus* and *Ac. volcanus* (Wetterer 1991b, 1993), I scored each load as fresh (soft, pliant, and green) or fallen (dry or yellowed) leaf material (fragment or whole leaf), herb section (stem or stem with leaves, leaf buds, or flowers), flower (part or whole), fruit (part or whole berry) or "other". Whenever possible, I determined the source of each piece of vegetation.

Finally, at each site I noted the presence and abundance of the other three species of leaf-cutting ants known to occur on the At-

Table 1 Forager size and load size in eight colonies of *Acromyrmex coronatus* compared with *Atta cephalotes* [S small colonies, $n=200$ (Wetterer 1994c); L large colonies, $n=900$ (Wetterer 1994b)], *Acromyrmex octospinosus* (from Wetterer 1991b), and *Acromyrmex volcanus* (from Wetterer 1993). Mean and range of forager mass (m_A in

mg), coefficient of variation of forager mass ($CV=\text{mean}/\text{variance}$), mean relative burden ($B=m_L/m_A$), and the logarithmic relation between ant mass and load mass (m_L in mg). *Acromyrmex* sample sizes as in Table 2. Load mass was not measured for *Ac. coronatus* colonies Z5 and Z6, and for small *A. cephalotes* colonies

	m_A+1 SD	Range	CV	$B+1$ SD	Log m_L regression	r^2
<i>Ac. coronatus</i>						
R1	2.8±0.6	0.9–4.3	0.20	1.9±0.8	0.3+0.8 log m_A	0.14*
R2	5.3±1.3	2.1–8.4	0.25	1.7±0.7	0.7+0.3 log m_A	0.04
Z1	3.3±1.2	1.8–5.8	0.36	1.1±0.6	0.2+1.2 log m_A	0.22**
Z2	2.3±0.8	1.2–4.9	0.34	1.9±2.0	0.2+0.8 log m_A	0.07
Z3	2.9±0.6	1.8–4.9	0.22	1.4±1.2	0.4+0.1 log m_A	0.00
Z4	4.2±1.7	1.8–9.0	0.40	0.9±0.7	-0.2+1.0 log m_A	0.21**
Z5	3.9±1.1	2.0–7.1	0.27	–	–	–
Z6	3.2±1.3	1.8–6.2	0.40	–	–	–
Total	3.4±1.4	0.9–9.0	0.41	1.5±1.2	0.1+0.8 log m_A	0.18**
<i>A. cephalotes</i> (S)						
<i>A. cephalotes</i> (L)	3.3±1.0	1.4–6.7	0.29	–	–	–
<i>A. cephalotes</i> (L)	7.3±4.1	1.4–32.1	0.56	3.0±1.4	0.6+0.8 log m_A	0.40**
<i>Ac. octospinosus</i>	13.3±4.2	4.0–21.2	0.31	1.4±1.2	-0.5+1.4 log m_A	0.16**
<i>Ac. volcanus</i>	30.6±4.3	19.1–41.5	0.14	1.2±1.0	-1.3+1.9 log m_A	0.08**

* $P<0.05$; ** $P<0.001$

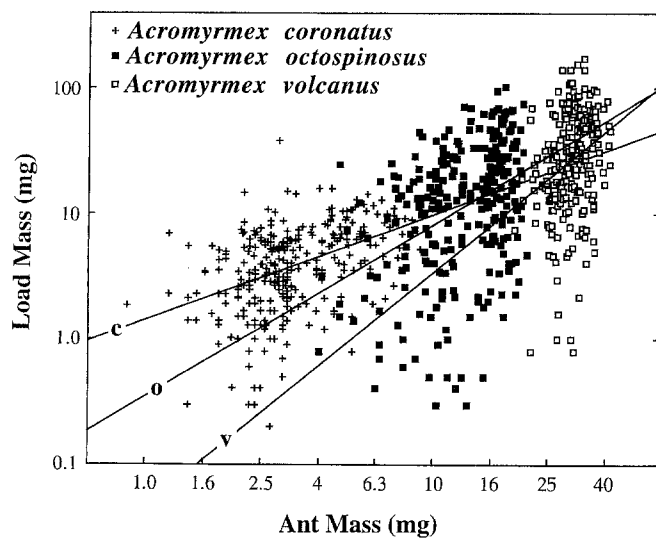


Fig. 1 Forager mass versus load mass for *Acromyrmex coronatus* ($n=295$) compared with *Acromyrmex octospinosus* ($n=275$; from Wetterer 1991b) and *Acromyrmex volcanus* ($n=239$; from Wetterer 1993). Regression equations are given in Table 1

lantic slope of Costa Rica: *A. cephalotes*, *Ac. octospinosus*, and *Ac. volcanus*.

Results

At El Plastico, I found no *Ac. coronatus* foragers, nor any sign of their activity, during the course of this study (though in 1992, I found several *Ac. coronatus* workers cutting herbs at El Plastico, but did not locate their foraging trail or nest). At both Rara Avis and Zurquí, *Ac. coronatus* foraging trails were common. I found *Ac. coronatus* damage almost exclusively on small herbaceous plants, particularly ferns, located in open areas cleared of trees and on slopes next to rivers. Occasionally, near *Ac. coronatus* nest entrances, I also found some minor damage on larger plants and small trees.

In total, I collected 380 laden *Ac. coronatus* foragers. The ants weighed from 0.9 to 9.0 μg , a tenfold range, although no individual colony showed more than a fivefold range (Table 1). Mean forager mass varied considerably

Table 2 Vegetation selectivity by foragers at eight colonies of *Acromyrmex coronatus* compared with the foraging selectivity of small (S) *A. cephalotes* colonies (from Wetterer 1994c), *Ac. octospinosus* (from Wetterer 1991b) and *Ac. volcanus* (from Wetterer 1993)

Colony	(n)	% Fresh leaf	% Fallen leaf	% Herb section	% Flower	% Fruit	% Other
<i>Ac. coronatus</i>							
R1	(50)	100	0	0	0	0	0
R2	(50)	100	0	0	0	0	0
Z1	(50)	46	42	0	10	0	2
Z2	(50)	84	4	0	10	2	0
Z3	(45)	40	40	9	0	0	11
Z4	(50)	86	2	10	0	2	0
Z5	(42)	100	0	0	0	0	0
Z6	(43)	100	0	0	0	0	0
Total	(380)	82	11	2	3	1	2
<i>A. cephalotes</i> (S)							
<i>A. cephalotes</i> (S)	(200)	97	0	0	1	1	1
<i>Ac. octospinosus</i>	(275)	23	17	9	19	27	5
<i>Ac. volcanus</i>	(239)	33	8	15	33	6	7

among colonies, from 2.3 ± 0.6 mg to 5.3 ± 1.3 mg (Table 1).

Combining data from all 295 *Ac. coronatus* foragers with weighed loads, I found that the logarithmic relationship between ant mass (m_A) and load mass (m_L) was an increasing function (Table 1; Fig. 1). Burden ($B = m_L/m_A$) had a mean of 1.5 and ranged from <0.05 to 6.7 (plus an outlier value of 13.3 for the one *Ac. coronatus* forager carrying a whole berry; Fig. 1). Although load mass for *Ac. coronatus* foragers was much smaller than load mass for *Ac. octospinosus* and *Ac. volcanus* foragers (Fig. 1), the mean burden was slightly higher for *Ac. coronatus* than it was for *Ac. octospinosus* and *Ac. volcanus* (Table 1). All three *Acromyrmex* species had much smaller mean burdens than did *A. cephalotes* (Table 1).

The majority (311 of 380=82%) of the *Ac. coronatus* foragers carried fresh leaf fragments or whole fresh leaves (Table 2). Most, if not all, of this fresh leaf material came from ferns, grass, and other small herbaceous plants. Only 14 or the 42 "fallen" or dry leaf fragments were cut from leaves fallen from trees, the rest were cut from dry grass or dead ferns. The ten pieces of flower material all appeared to come from grass and other small herbs. The two pieces of collected fruit material were one berry and one fruit fragment, probably both fallen from trees. Of the six loads categorized as "other," one was a piece of moss and five were unidentified lumps. Thus, about 95% (358 of 375) of the identified material collected by the ants appeared to come from small herbaceous plants.

The make-up of the loads at the eight individual colonies can be summarized as follows. At colony R1, the 48 of 50 foragers carried fern leaf fragments. At colony R2, half of the 50 leaf fragments came from ferns, and the other half from a variety of herbs. At colony Z1, foragers cut fresh fragments from a wide variety of grasses and small herbaceous plants. In addition, many foragers carried pieces of dry fern leaves, apparently cut from the dead fern plants that were very common in the area around the nest. Foragers from colony Z2 primarily cut fragments of small herbs within the forest. Foragers from colony Z3 were cutting herbs and also leaves fallen from trees planted in the lawn. At colony Z4, foragers cut exclusively fresh fragments from grasses and small herbaceous plants. At colonies Z5 and Z6, all foragers carried fragments cut from the abundant *Gunnera* plants nearby.

Trails of *Ac. coronatus* were often heavily frequented, with 5–80 laden foragers per meter of trail. At larger colonies, the main foraging trails were well-defined and cleared of all obstacles, much like the trunk trails of comparably-sized *A. cephalotes* colonies.

I commonly observed *Ac. coronatus* minima workers traversing the trails without burdens, and occasionally riding as hitchhikers on the loads of foragers. At colony Z2, I observed minima workers on leaves of plants that appeared to be guarding the larger workers as they cut the leaves. At this same colony, 5 of the 50 laden ants I collected were accompanied by hitchhikers. The mean

mass of these five hitchhikers was 1.0 ± 0.2 mg, less than half the mean mass of laden foragers at this colony. The minima guards and hitchhikers presumably protect larger foragers against attack by parasitic phorid flies. At colony R1, I observed a number of phorid flies hovering over the trail near a nest entrance (also see Weber 1946).

Locating the fungus gardens of *Ac. coronatus* proved to be difficult because the nest entrances were often far from the actual nest. In the larger colonies, foraging trails passed for ten m or more just below the surface of the ground before reaching the ants' fungus garden. At colony Z1, I spent 2 days digging up the ants' meandering underground foraging trail in a failed attempt to locate their nest.

I located and excavated two *Ac. coronatus* nests, those of colonies Z3 and Z4. Both nests were in the ground directly under a thatched mound of dry vegetation, such as has been described in earlier studies (Weber 1946; Gonçalves 1967; Fowler 1979, 1985). Colony Z3 showed no sign of cleared trunk trails and had two nest entrances directly at the side of the nest. At colony Z4, I found two major trunk trails that entered the ground more than ten m from the nest.

Colony Z3 was much smaller than colony Z4. I counted 17596 workers from colony Z3, whereas, based on counting ants in subsamples of the entire nest, I estimated that colony Z4 had considerably more than 150000 workers.

In addition to the variation in density of *Ac. coronatus* described earlier, the densities of the three other leaf-cutting ant species found on the Atlantic slope of Costa Rica varied greatly among study sites. At La Selva *A. cephalotes*, *Ac. octospinosus*, and *Ac. volcanus* all were common (Wetterer 1991b, 1993). At El Plastico, *A. cephalotes* and *Ac. volcanus* were both common and conspicuous (see Wetterer 1993), whereas *Ac. octospinosus* was rare. During the study, I found no *Ac. octospinosus* at El Plastico, though in 1992, I found one colony. At Rara Avis, *Ac. volcanus* colonies were common in forest. I also found one colony each of *A. cephalotes* and *Ac. octospinosus*. At Zurquí, *Ac. coronatus* was the only leaf-cutter species that I found.

Discussion

Forager size and foraging selectivity

Intra- and interspecific differences in forager polymorphism among leaf-cutting ants in Costa Rica appear to relate to differences in the economics of harvesting preferred resources. Forager size and foraging selectivity in *Ac. coronatus* are similar to those of small *A. cephalotes* colonies. Like *Ac. coronatus*, small *A. cephalotes* colonies have small foragers (Table 1) that harvest the thin, soft leaves of the herbs (Table 2; Wetterer 1994c). In large *A. cephalotes* colonies, however, a wider size-range of workers are used (Table 1) in harvesting the leaves of trees, with larger workers cutting thicker, tougher leaves

(Wetterer 1994b). Because small *A. cephalotes* workers are more efficient at harvesting the thin, soft leaves and large workers are more efficient at harvesting thick, tough leaves, the match of forager size to leaf type (both ontogenetically and behaviorally) increases overall foraging efficiency (Wilson 1980b; Wetterer 1994b, c). Extreme forager polymorphism in large *A. cephalotes* colonies appears to broaden the diversity of tree species that they can exploit efficiently (Wetterer 1994b).

Ac. octospinosus and *Ac. volcanus* have large, relatively monomorphic foragers (Table 1) that appear to be well suited as generalist foragers, able to cut or collect any desirable vegetation encountered (Wetterer 1991b, 1993). For species such as *Ac. octospinosus* and *Ac. volcanus* that depend primarily on cutting or collecting vegetation at small, ephemeral sources, matching worker size to resource type during the short duration of each attack at an individual source may be economically impractical. Employing a forager caste of workers that are large enough to cut or collect any desirable vegetation encountered may be more efficient (see Wetterer 1993 for discussion of differences between *Ac. octospinosus* and *Ac. volcanus*).

Trunk trails and hitchhikers

Ac. coronatus shares other traits with *A. cephalotes*. In both species, larger colonies maintain trunk trails which they keep cleared of obstructions. These trunk trails allow large numbers of foragers to travel quickly to distant vegetation sources (Fowler 1978). High levels of foraging activity on trunk trails, however, may make foragers more apparent and therefore more susceptible to attack by natural enemies, such as parasitic phorid flies. *Ac. coronatus* and *A. cephalotes* both have minima workers that hitchhike on loads and presumably protect the foragers from attack by phorid flies. The subsurface trails of *Ac. coronatus* may serve as an additional defense against attack. Subsurface trails have been noted in several other species of leaf-cutting ants (*Atta sexdens* – Fowler 1985, Vasconcelos 1990; *Atta mexicana* – Mintzer 1979; *Atta texana* – Wetterer, personal observation; *Acromyrmex ambiguus*, *Acromyrmex crassispinus*, *Acromyrmex lundii*, *Atta saltensis*, *Atta capiguara* – Fowler 1985). Fowler (1985) did not include *Ac. coronatus* among those species in Paraguay having trunk trails and subsurface trails. It is possible that Fowler (1985) examined only small colonies. Alternatively, *Ac. coronatus* may show geographic variation in these traits.

Ac. octospinosus and *Ac. volcanus* have inconspicuous and ill-defined foraging trails, although often their foraging trails take advantage of cleared areas such as vines, logs, and sidewalks (personal observation). Also, I have observed laden *Ac. octospinosus* foragers traveling along the edge of wide *A. cephalotes* trunk trails at times when *A. cephalotes* foraging levels were low. However, each time an *Ac. octospinosus* forager encountered an *A. cephalotes* worker, the *Ac. octospinosus* forager quickly

ran off the trail and froze. *Ac. octospinosus* and *Ac. volcanus* foragers typically react this way to disturbance (Wetterer 1993), but I have not observed this “timid” behavior in *Ac. coronatus* or *A. cephalotes*. Establishing and maintaining cleared trunk trails may not be economically worthwhile for *Ac. octospinosus* and *Ac. volcanus* due to their small colony size and corresponding small number of foragers, typically only one or two foragers per meter of trail. Minima guards also may not be effective due to the wide spacing of foragers needing protection, although low forager traffic may also make the foragers less conspicuous and therefore less vulnerable to attack. In the absence of minima guards, avoidance and hiding behavior may serve as the primary defense that *Ac. octospinosus* and *Ac. volcanus* foragers use against attack by parasites and predators

Distribution and competition among leaf-cutting ants in Costa Rica

In Costa Rica, *Ac. coronatus* and *A. cephalotes* appear to show little overlap in geographic distribution. *Ac. coronatus* is the dominant leaf-cutter at higher elevation sites such as Rara Avis, Zurquí, and Monteverde, where *A. cephalotes* colonies are uncommon or absent. Conversely, *Ac. coronatus* is uncommon or absent at lower elevation sites such as La Selva and El Plastico, where *A. cephalotes* is common. Differences in the distribution of *Ac. coronatus* and *A. cephalotes* could simply be due to interspecific differences in climate tolerances or other habitat requirements. Indeed, Fowler (1983) concluded that climate and habitat complexity influenced the distribution of leaf-cutting ants in Paraguay. Fowler (1983), however, proposed that the most important factor determining the local abundance of leaf-cutting ant species was interspecific competition. Fowler (1983) found that at sites where *Acromyrmex* species were locally abundant, *Atta* species were rare or absent, and vice versa. Such negative associations were most common among species with similar foraging habits. Both exploitative and interference competition could be involved. In interference competition, *Ac. coronatus* colonies would seem to be at a disadvantage against mature *A. cephalotes* colonies which are larger and possess a specialized soldier caste. Mature *Atta* colonies commonly destroy the smaller nests of other leaf-cutting ants (Fowler et al. 1986; Fowler 1992). In this way, mature *A. cephalotes* colonies may exclude *Ac. coronatus* colonies from preferred lowland areas. Conversely, in areas where they dominate, large *Ac. coronatus* colonies may be able to prevent the establishment of young *A. cephalotes* colonies.

Curiously, *Ac. octospinosus* and *Ac. volcanus* are common at lower elevation sites, such as La Selva, despite high densities of *A. cephalotes* (Wetterer 1991b, 1993). *Ac. octospinosus* and *Ac. volcanus* may be able to avoid most contact with *A. cephalotes* due to their differences in resource preferences and their inconspicuous foraging habits. Whether *Acromyrmex* species are more

abundant in lowland Costa Rican sites in the absence of *A. cephalotes* is unknown. More thorough studies of the distribution and abundance of leaf-cutting ants in Costa Rica are needed.

Future directions

The present study indicates that differences in forager size appear to have important implications for the foraging ecology and niche separation among Costa Rica leaf-cutting ants. For a more complete understanding of the significance of interspecific variation in leaf-cutting ants, however, analyses of forager size and foraging ecology need to be extended to others of the approximately 40 described species of leaf-cutting ants. The one other *Atta* species in Costa Rica, *Atta colombica* Guérin, occurs only on the Pacific slope and appears to have similar foraging patterns as *A. cephalotes* (Rockwood 1976; J.K. Wetterer, to be published). Many species of *Atta* and *Acromyrmex* in South America, however, harvest primarily grass (Fowler et al. 1986, 1989). On the basis of economic considerations, I predict that the forager polymorphism in mature colonies of these grass-harvesting species should be similar to that found in *Ac. coronatus* and in small *A. cephalotes* colonies.

The ecological significance of intraspecific variation in forager size in leaf-cutting ants deserves greater attention. In *A. cephalotes*, such variation seems to have important adaptive significance. Both the change in forager size with colony size and the use of different-size foragers at different vegetation sources appear to increase foraging efficiency (Wilson 1980b, 1983a, b; Wetterer 1994b, c). In addition, *A. cephalotes* colonies use different-size foragers at different times of day, apparently as a defense against phorid flies (Wetterer 1990a; Orr 1993). *Acromyrmex* species also show variation among colonies in forager mass [range of colony means: *Ac. coronatus*: 2.3–5.3 mg; *Ac. octospinosus*: 8.8–17.9 mg (Wetterer 1991b); *Ac. volcanus*: 25.8–34.6 mg (Wetterer 1993)]. In the present study, the smaller *Ac. coronatus* colony (Z3) had a mean forager mass of 2.9 mg, whereas the larger colony (Z4) had a mean forager mass of 4.2 mg, suggesting that colony size may influence forager size in *Acromyrmex* species. Many other factors also may affect forager size in leaf-cutting ants. It remains to be seen whether leaf-cutters can make adaptive long- or short-term changes in forager size in response to such factors as local weather conditions, resource availability, or presence of competitors.

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