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# Foraging Ecology of the Desert Leaf-Cutting Ant, *Acromyrmex versicolor*, in Arizona (Hymenoptera: Formicidae)

by

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## ABSTRACT

The desert would seem to be an inhospitable place for leaf-cutting ants (*Acromyrmex* spp. and *Atta* spp.), both because the leaves of desert perennials are notably well-defended, both chemically and physically, and because leaf-cutters grow a fungus that requires constant high humidity. We investigated strategies that leaf-cutters use to survive in arid environments by examining foraging activity, resource use, forager size, load size, and nesting ecology of the desert leaf-cutting ant, *Acromyrmex versicolor*, at 12 colonies from 6 sites in Arizona during June, August, and November 1997, and March 1998.

The ants showed striking seasonal changes in materials harvested, apparently in response to changes in the availability of preferred resources. *Acromyrmex versicolor* foragers (n = 800) most commonly collected dry vegetation (54.3% of all loads), but also harvested ephemeral resources, such as dry flowers (18.6%), fresh young leaves (18.5%), fruits and seeds (4.0%), and fresh flowers (3.5%), when seasonally available. Most dry leaf material came from perennial shrubs and trees, including paloverde (*Cercidium floridum* and *Cercidium microphyllum*), ironwood (*Olneya testota*), catclaw acacia (*Acacia greggii*), mesquite (*Prosopis velutina*), and creosote (*Larrea tridentata*). Foragers, however, never harvested mature leaves of desert perennials despite a year-round abundance. Foragers ranged 13-fold in mass (0.8 - 10.6 mg; mean =  $5.3 \pm 1.8$  mg). Mean load mass was 0.9 times ant mass, which is lower than found for tropical leaf-cutters. This may relate to the dried nature of most material harvested and the small leaflet size of desert plants.

By harvesting fallen dry leaves, desert leaf-cutters may circumvent chemical defenses found in fresh mature leaves, but this strategy has complications. Adult workers of some tropical leaf-cutters appear to obtain almost all of their carbohydrates from drinking sap while cutting

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fresh leaves. Because *Acromyrmex versicolor* foragers harvest no fresh plant material for much of the year, they must depend on other sources for carbohydrates. Also, dry vegetation offers little moisture for the leaf-cutters' drought-sensitive fungus gardens, therefore these ants may need additional sources of water. We observed *Acromyrmex versicolor* foragers feeding at extrafloral nectaries of *Opuntia* cacti, though the importance of this resource is unclear.

**Key Words** *Acromyrmex*, Arizona, Desert, Desert Perennials, Foraging

## INTRODUCTION

Ants of the Tribe Attini are unique among ants in their habit of growing fungus for food. All attines are obligately dependent on the fungus. In other aspects of their biology, however, attines vary greatly (Wheeler 1907; Weber 1972; Hölldobler and Wilson 1990). Species of nine "lesser" attine genera, *Apterostigma*, *Cyphomyrmex*, *Mycetarotes*, *Mycetophylax*, *Mycetosoritis*, *Mycocepurus*, *Myrmicocrypta*, *Sericomyrmex*, and *Trachymyrmex*, tend to have small colonies (< 5000 workers) and use insect carcasses and excrement or pieces of dry plant material as substrate for their fungus gardens. In contrast, attine ants of the genera *Acromyrmex* and *Atta*, called "leaf-cutting ants," have colonies that can grow to include tens of thousands to several million workers and commonly harvest fresh vegetation. Wilson (1986) considered the adaptation in leaf-cutting ants that allowed "efficient utilization of almost all forms of fresh vegetation" so unique and successful "that it can be properly called one of the major breakthroughs in animal evolution."

Although use of fresh vegetation is often thought of as a distinguishing trait of leaf-cutting ants, not all leaf-cutting ants harvest primarily fresh vegetation. For example, the desert leaf-cutting ants *Acromyrmex versicolor* and *Atta mexicana* harvest primarily dry plant material (Gamboa 1975a; Mintzer 1979, 1994), a habit shared with many lesser attines. In fact, desert leaf-cutters may even actively desiccate leaves before adding them to their fungus garden. Wheeler (1907) noted that *Ac. versicolor* foragers dropped "considerable quantities" of harvested leaves along the their foraging path, and left them "to wither in the sun." This apparent preference for dry material seems surprising to find in species that live under conditions where moisture is scarce. As Wheeler (1907) pointed out, the desert "is certainly a remarkable environment for an ant compelled to subsist on fungi that can grow only in a humid atmosphere, an ant, moreover, belonging to a group which probably first developed in the rain-forests of the tropics."

In the present study, we investigated strategies a desert leaf-cutter, *Ac. versicolor*, use to survive in arid environments by evaluating their foraging activity, resource use, forager polymorphism, load size, and nesting ecology and comparing them with those of other species of leaf-cutting ants.

## METHODS

We studied the foraging of 12 *Acromyrmex versicolor* colonies at 6 sites, of similar elevation, northeast, north, and west of Tucson, Arizona, between 1 June 1997 and 28 March 1998. Colonies A, B, C, and H were in Oro Valley (32°22'N, 110°58'W; elevation 840 m); colonies D, I, J, and L were on the property of the Sonoran Arthropod Studies Institute (SASI), surrounded by Tucson Mountain Park (32°14'N, 111°07'W; elevation 900 m); colony E was 5 km north of Tanque Verde (32°17'N, 110°45'W; elevation 840 m); colony F was 0.5 km south of Oro Valley (32°21'N, 110°58'W; elevation 810 m); colony G was next to Agua Caliente Wash, 1 km SE of colony E (32°17'N, 110°44'W; elevation 810 m); colony K was on the property of Biosphere 2 Center between Oracle and Oracle Junction (32°33'N, 110°51'W; elevation 1000 m).

The colonies were distributed in a variety of habitats. Colonies A, B, C, E, and H sites were in “desert-landscaped” residential areas with both intact and planted native vegetation; colonies F, G, and K were in somewhat disturbed desert in residential areas; colonies D, I, J, and L were in relatively undisturbed desert.

We sampled foraging in June 1997 (colonies A, B, C, D, E, F and G), August 1997 (colonies A, B, C, D, E, F, and H), November 1997 (colonies A, B, C, D, E, F, H, I, J, and K), and March 1998 (colonies A, C, D, E, F, K, and L). During each study period, we collected at all colonies that had sufficient foraging activity.

For each sample, we collected 25 consecutive laden ants, or at 10-second intervals if traffic was high, as they passed a set point on their foraging trail. We placed each ant with her load in a separate vial and temporarily anesthetized the ants by placing the vials in a freezer for several minutes.

We scored each load as fresh or dry leaf material, fresh or dry herb section (including straw), fresh or dry flower (part or whole), fruit (part or whole cactus fruit, seed pod, or seed husk), seed, or “other” (bird frass, insect frass, or snake skin molt). Whenever possible, we determined the specific plant source of each piece of vegetation.

We measured the mass of each ant ( $\underline{m}_A$ ) and each load ( $\underline{m}_L$ ) to the nearest 0.1 mg on a Mettler balance. We calculated burden ( $\underline{B}$ ) as  $\underline{m}_L / \underline{m}_A$ . After weighing, we returned the ants to their nest entrance.

## RESULTS

### Foraging activity

*Acromyrmex versicolor* showed striking seasonal change in foraging activity (also see Murray 1972, Gamboa 1976). During the hot summer sampling periods of June and August, *Acromyrmex versicolor* foraging activity was entirely nocturnal. In cooler November, foraging activity was entirely diurnal. In warming March, most foraging activity was diurnal, but at least three colonies had some nocturnal activity as well.

At all study colonies, we did not find the ants foraging every time we visited. We often observed workers milling around the nest entrance but doing little or no foraging. We often had to return many times before we found ants foraging in appreciable numbers. In August, November, and March we never observed activity at colony G. In March, there was also no activity at colonies B, H, and I; colony J had few foragers active and was not sampled.

### Resource use

In total, we collected 32 samples of 25 laden ants and their loads ( $n = 800$ ). Foragers harvested the dry leaves in substantial quantities year-round (Table 1, Fig. 1), but also foraged on more ephemeral resources when they became available. In June, foragers primarily collected dry flower (73.7%) and dry leaf material (20.0%). In addition, the ants collected small amounts of grass straw (2.2%), plus one small seed pod, one small seed husk, three seeds, one dry woody twig, and one fragment of molted snake skin. No colony harvested any fresh plant material. In August, the ants harvested a mix of resources including dry leaf material (30.5%), dry straw and herb stems (22.0%), newly-flushed fresh leaves cut from trees and shrubs (21.5%), dry flower material (9.5%), fruit fragments and seed pods (8.0%), seeds (5.5%), and bird droppings and insect frass (3.0%). In November, foragers almost exclusively harvested leaf material, both dry leaves (78.4%) and newly-flushed fresh leaves (20.4%), primarily from trees. In addition they

Table 1. *Acromyrmex versicolor* resource use (% of loads) during different time of the year.

Month	Fresh eaf/stem flower		Dry leaf/stem flower		fruit & seed	non-plant
June	0.0	0.0	22.9	73.7	2.9	0.6 (1 molt)
August	21.5	0.0	52.5	9.5	13.5	3.0 (6 frass)
November	20.8	0.0	78.8	0.0	0.0	0.4 (1 frass)
March	30.3	16.0	52.0	0.6	0.0	1.1 (2 frass)
Total	18.5	3.5	54.3	18.6	4.0	1.3

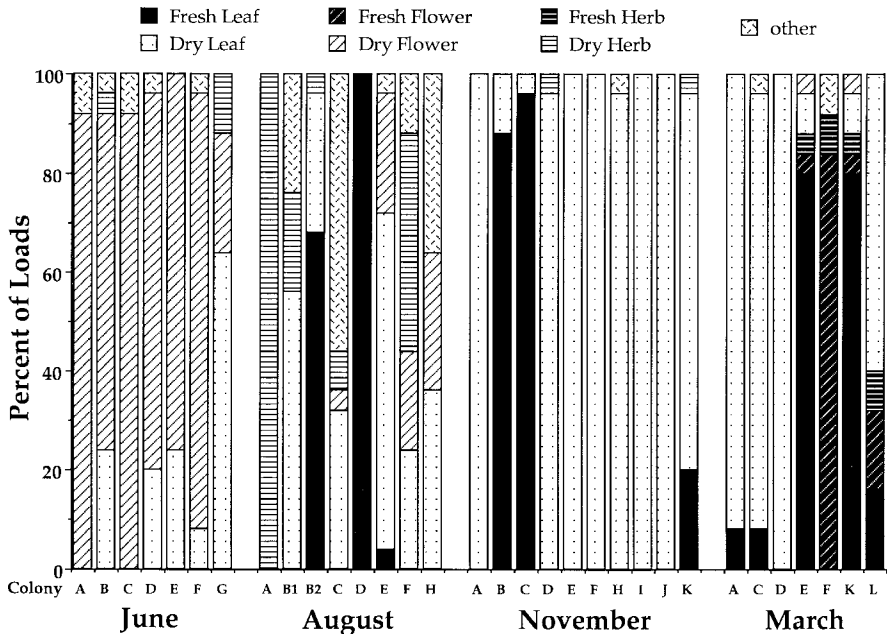


Fig. 1. Resources harvested of 800 *Acromyrmex versicolor* foragers from 12 colonies (A - L) at 4 different times of years. For each collection,  $n = 25$ . (Two August collections were made for colony B.)

collected two herb stems (one dry and one fresh) and one piece of insect frass. Much of the dried leaf material appeared to have been knocked to the ground by recent rains. In March, foragers again harvested a mix of resources including dry leaf material (50.9%), fresh leaves cut from herbaceous plants (27.4%), dry and fresh flower material (16.6%), dry and fresh herb stems (3.4%), and insect frass (1.2%). Three of seven colonies harvested primarily fresh plant material: two colonies cut primarily the fresh leaves of desert ephemerals and one colony cut primarily fresh flowers from a desert mistletoe (*Phoradendron californicum*) growing in a white thorn acacia (*Acacia constricta*).

For all seasons combined, foragers collected primarily dry vegetation (54.3% of all loads; Table 1; Fig. 1), but also harvested dry fallen flowers (18.6%), fresh young leaves (18.5%), fruits and seeds (4.0%), and fresh flowers (3.5%). The ants also collected small amounts of bird and insect frass and one piece of molted snake skin (Table 1). In 20 of the 32 samples (62.5%), none of the 25 foragers harvested any fresh plant material (leaves, stems, or flowers) (Fig. 1). In only eight of the 32 samples did more than 20% of the foragers harvest fresh vegetation, but in six of these cases, the shift to harvesting fresh plant material was

almost complete (Fig 1). Plant material came from many species of desert perennials, well as shrubs, grasses, and herbs (Table 2). In total, 68.8% of the loads were from seven species of desert perennials: paloverde (*Cercidium floridum* and *Cercidium microphyllum*), ironwood (*Olneya testota*), catclaw acacia (*Acacia greggii*), mesquite (*Prosopis velutina*), creosote (*Larrea tridentata*), ocotillo (*Fouquieria splendens*) (Table 2).

### Forager and load size

There was a 13-fold range in forager mass (Table 3; range = 0.8 - 10.6 mg; mean mass =  $5.3 \pm 1.8$  mg). Mean forager mass varied two-fold among samples (3.5 - 7.3 mg).

Load mass ranged from 0.1 - 91.1 mg. The lightest loads were dried flower parts, dry grass fragments, and single dried leaflets. The heaviest loads were flower buds, whole flowers, seed pods, twigs, frass, and fresh yellow paloverde petioles with up to 14 leaflets.

Burden ( $\frac{m_L}{m_A}$ ) ranged from 0.02 to 14.23 (Table 3). Burden changed with season, averaging 0.8 in June, increasing to 1.6 in August, and decreasing to 0.7 in November and March (Table 3). The increase in August was largely due to the inclusion of a few very large loads including 13 loads over 30 mg: seed pods (37.6, 42.3, 43.3, 45.5, 57.1, 62.2 mg), twigs (32.6, 38.3, 43.8 mg), frass (34.7, 35.6, 36.8 mg), and a piece of *Opuntia* fruit (91.1 mg).

Within most of the 32 samples there was a positive relationship between forager mass and load mass, with forager mass explaining up to 52% of the variance in load mass. Overall, however, there was only a weak correlation between forager mass and load mass (Table 3;  $R^2 = 0.07$ ,  $p < 0.05$ ). This was because load mass also depended strongly on the type of resource being harvested, and this varied among colonies and seasons.

In all seasons, we observed many workers returning to the nest not carrying a load. In March, we observed and photographed large numbers of *Ac. versicolor* foragers from colony D climbing on *Opuntia* cacti. The ants appeared to be feeding at the base of spines on nectar from extrafloral "thorn nectaries" (Pickett and Clark 1979; Oliveira *et al.* 1999), and then returning to the nest without any other load beyond, we presume, the liquid in their crops.

### Nesting

Eleven of the 12 *Ac. versicolor* colonies occurred in areas with greater water supplies relative to the surrounding areas. Eight colonies were in residential areas within foraging distance of artificially watered desert vegetation (A, B, C, E, F, G, H, and K), and two of these colonies (G and

Table 2. *Acromyrmex versicolor* resource use (% of loads) for parts of different plant species.

Species	Fresh		Dry		fruit & seed	total
	leaf/stem	flower	leaf/stem	flower		
<i>Cercidium</i> spp.	6.3	-	8.4	7.9	-	22.5
<i>Olneya testota</i>	3.1	-	10.4	2.4	0.1	16.0
<i>Acacia greggii</i>	-	-	8.0	3.1	-	11.1
<i>Prosopis velutina</i>	-	-	8.1	-	1.3	9.4
<i>Larrea tridentata</i>	-	-	6.8	-	-	6.8
<i>Fouquieria splendens</i>	2.1	-	0.9	-	-	3.0
Other species	7.0	3.5	11.8	5.3	2.5	30.0

K) were next to running water (a river and a drainage channel). Of the four colonies in relatively undisturbed desert, two (D and L) were next to arroyo channels where water flows after heavy rains, and one (J) was within foraging distance of a building with watered gardens.

In June, we attempted to excavate colony C using shovels. Over the course of several hot days, we dug a hole in the hard packed earth more than 1.5 m deep and 1 m across, but we did not find the fungus garden. When we finally stopped digging, the ants soon reappeared and continued to forage from an entrance at the bottom of our hole.

### Other observations

We observed no small workers riding on loads (“hitchhikers”) in *Ac. versicolor*, as have been recorded for several other leaf-cutting ant species, including *Atta cephalotes* and *Acromyrmex coronatus* (Wetterer, 1990, 1995).

In November, we noted several dealate *Ac. versicolor* gynes outside the nest entrance of colony F. We witnessed a worker carry a dealate gyne out of this nest. Gamboa (1975b) also recorded *Ac. versicolor* ejecting conspecific gynes from colonies, but could not decipher the significance of this behavior. It seems likely that these gynes are virgins who have dropped their wings and stayed in their natal colony, rather

Table 3. Forager size and load size for *Acromyrmex versicolor* colonies during different time of the year. Mean and range of forager mass ( $m_A$  in mg), mean relative burden ( $B = m_L/m_A$ ), and the logarithmic relation between ant mass and load mass ( $m_L$  in mg).

Month	$m_A \pm 1$ SD	range	$B \pm 1$ SD	$\log m_L$ regression	$R^2$
June	$5.6 \pm 1.9$	1.2 - 10.6	$0.8 \pm 0.9$	$-0.2 + 0.7 \log m_A$	0.05
August	$5.6 \pm 1.8$	1.4 - 9.5	$1.6 \pm 2.0$	$0.0 + 0.9 \log m_A$	0.10
November	$4.8 \pm 1.8$	0.8 - 8.6	$0.7 \pm 0.5$	$0.0 + 0.5 \log m_A$	0.07
March	$5.1 \pm 1.8$	1.2 - 9.7	$0.7 \pm 1.1$	$-0.3 + 0.7 \log m_A$	0.06
Total	$5.3 \pm 1.8$	0.8 - 10.6	$0.9 \pm 1.3$	$-0.1 + 0.8 \log m_A$	0.07



than mated gynes in a polygynous colony (see Rissing *et al.*, 1986).

Other large ants at the study sites were several species of seed-harvesting ants, *Pogonomyrmex* spp. and *Aphaenogaster* spp. We once noted *Ac. versicolor* workers in antagonistic interactions with an *Aphaenogaster cockerelli* worker. When an *Aph. cockerelli* worker carried a piece of bird dropping across a trail of *Ac. versicolor*, several *Ac. versicolor* workers repeatedly attacked the *Aph. cockerelli* worker and eventually drove it off. Gamboa (1975b) noted that *Aph. cockerelli* appeared to be an important predator on *Ac. versicolor* queens.

## DISCUSSION

### Resource use by desert leaf-cutting ants

Throughout the year, *Ac. versicolor* foragers collected considerable amounts of dry leaves from desert perennials, but also, when available, commonly harvested flowers and flushing leaves, resources often preferred by other leaf-cutter species (Rockwood 1976, Littledyke and Cherrett 1978; Stradling 1978; Howard 1987, 1988; Sales 1994). In June, all *Ac. versicolor* colonies collected substantial amounts of dry flowers, fallen to the ground in abundance after the spring bloom. In August, as the supply of dry flowers became exhausted, ants started harvesting a variety of newly available resources, including seeds, fruit, and fresh flushing leaves of trees. In November, most colonies foraged almost exclusively on dry leaf material, though two colonies harvested primarily fresh young leaves flushing on nearby trees. In March, four colonies primarily collected dry leaf material, but three colonies harvested mostly fresh plant material, the leaves and flowers of desert spring ephemerals and the flowers of a blooming desert mistletoe (*Phoradendron californicum*). *Acromyrmex versicolor* foragers never harvested the mature leaves of desert perennials, despite a year-round abundance of this resource, yet harvested substantial quantities of dry leaves from these same plant species.

Although he did not present quantitative data, Gamboa (1975a) found a qualitatively similar seasonal shift in resource use by four *Ac. versicolor* colonies at a site 50 km northeast of Tempe, Arizona. Ants took only dry plant material in early July, a mix of dry and fresh material from mid-July to the end of September, only dry plant material in October through early November, a mix in mid-November, and exclusively fresh material in mid-December. Gamboa (1975a) noted that the ants harvested more fresh vegetation after periods of heavy rain in mid-July and mid-November. Gamboa (1975a) found that although the ants

harvested a wide variety of vegetation, the “bulk of the forage” consisted of dry grass straw. In contrast, we found that the ants harvested significant amounts of dry grass only in August and, overall, dry grass made up less than 5% of the loads. This difference between studies may relate to resource availability. Gamboa’s (1975a) study site was used for cattle-grazing, unlike any sites in our study, and presumably had more grass cover.

*Atta mexicana*, a desert leaf-cutting ant that reaches its northern limit in southernmost Arizona (Mintzer and Mintzer 1988), shows seasonal resource use very similar to that of *Ac. versicolor* (Mintzer 1979, 1994). Mintzer (1979) found that “dry leaves dropped by preferred perennial plant species comprised a major fraction of the material collected” by *A. mexicana*. Mintzer (1979, 1994) also noted that *A. mexicana* showed a seasonal change in resource use based on the availability of preferred resources, shifting to newly flushing leaves or dry fallen flowers when available.

The desert leaf-cutter’s preference for dry leaf material over fresh mature leaves may relate to chemical defenses in the leaves. Drying may make mature perennial leaves more palatable to desert leaf-cutters due to repellent chemical defenses breaking down when the leaves are dried and baked in the desert sun. In addition, perennial plants may export repellent chemicals from their leaves before dropping them. For example, Hubbell *et al.* (1984) found that shortly before the start of the dry season in a Costa Rican semideciduous dry forest, when many plants dropped their leaves, almost all plant species showed a dramatic decline in the level of extractable chemicals known to be repellent to leaf-cutters.

Loss of repellency in dry leaves may be particularly important to desert leaf-cutters because the leaves of desert perennials are so well-defended chemically (e.g., Meyer and Karasov 1989). Plant defense theory predicts that plants with resource-limited growth should invest more in plant defense because the cost of replacing lost vegetation is higher (Coley *et al.* 1985).

The use of dry vegetation ability as a fungal substrate is a primitive characteristic that *Ac. versicolor* and *A. mexicana* share with many lesser attine ants. Many lesser attine ant species are known to harvest fallen dry vegetation but not fresh leaves (Wheeler 1907; Weber 1972; Schumacher and Whitford 1974; Waller 1989; Hölldobler and Wilson 1990), possibly because they are similarly unable to overcome the higher levels of chemical defenses in fresh leaves (see Vasconcelos and Cherrett 1996).

### Resource use by other leaf-cutting ants

Several leaf-cutting ant species in semiarid habitats show resource usage similar to that of desert leaf-cutters, though ants in semiarid habitats also harvest some fresh mature leaves. For example, Farji-Brener and Protomasto (1992) found that *Acromyrmex striatus* foragers in a subtropical Argentine dry forest took almost exclusively dry and mature leaves in the fall (78% dry leaves, 20% mature leaves), but a greater mix in the spring (27% dry leaves, 2% mature leaves, 25% young leaves, 32% flowers, 15% fruit) and summer (51% dry leaves, 12% mature leaves, 16% young leaves, 8% flowers, 14% fruit). Farji-Brener and Protomasto (1992) found that *Acromyrmex hispidus* foragers in the same habitat showed a similar shift between fall (55% dry leaves, 19% mature leaves, 4% young leaves, 21% flowers, 3% fruit) and spring (30% dry leaves, 7% mature leaves, 17% young leaves, 10% flowers, 37% fruit).

Even in more humid tropical forests, many leaf-cutters do not harvest primarily on fresh leaves (Table 4). For example, *Acromyrmex octospinosus* and *Acromyrmex volcanus* colonies in Costa Rica often scavenge on broad range of resources year-round, with less than half their harvest fresh leaves and stems (Table 4; Wetterer 1991, 1993; Wetterer *et al.* 1998), though the fallen plant material harvested by these species was generally much less desiccated than the fallen material harvested by *Ac. versicolor* (J.K.W., pers. obs.). Some tropical leaf-cutter species harvest primarily fresh leaves for only part of the year. For example, Wirth *et al.* (1997) found that *Atta colombica* in a semideciduous forest in Panama foraged almost exclusively on fresh leaves along with some flower petals in the wet season, but shifted to taking as little as 20% fresh leaves in the dry season, foraging instead primarily on flowers and fallen *Ficus* stipules, supplemented with fruit in the late dry season. Vasconcelos (1990) found that two *Atta sexdens* colonies in Brazil showed great shifts in resource use at different times of year, alternatively depending primarily on fresh young leaves, fresh mature leaves, dry leaves, or flowers.

*Atta cephalotes*, perhaps the best studied leaf-cutting ant, cuts primarily fresh leaves, but also harvests fresh flowers when available (Table 4; Cherrett 1972; Vasconcelos 1990). Cherrett (1972) found that *A. cephalotes* foragers in Guyana harvested small amounts of dry vegetation (3.6% of loads) "probably obtained whilst clearing the trail of litter." Vasconcelos (1990) found that fresh leaves made up 98% of the harvest of two *A. cephalotes* colonies in Brazil. Such selectivity among leaf-cutting ants in general, however, may be more the exception than the rule.

Table 4. Resources harvested by *Acromyrmex versicolor* compared with that of four species of leaf-cutting ants from Costa Rica: *Acromyrmex coronatus* (Wetterer, 1995), *Acromyrmex octospinosus* (Wetterer, 1991), *Acromyrmex volcanus* (Wetterer, 1993), and *Atta cephalotes* (Wetterer, 1994). Category divisions match those of earlier studies.

Species	(n)	% fresh leaf	% fallen leaf	% herb part	% flower	% fruit	% other
<i>Ac. versicolor</i>	(800)	18	48	7	22	3	3
<i>Ac. coronatus</i>	(380)	82	11	2	3	1	2
<i>Ac. octospinosus</i>	(275)	23	17	9	19	27	5
<i>Ac. volcanus</i>	(239)	33	8	15	33	6	7
<i>A. cephalotes</i>	(200)	97	1	1	1	0	0

### Alternative sources for carbohydrates and water

Although using dry vegetation may allow desert leaf-cutters and other attine ants to avoid some of the toxic effects of plant defenses, this strategy has some obvious disadvantages. Early researchers thought that the attines' fungus constituted the sole food source for both larval and adult workers (Weber 1972). Littleddyke and Cherrett (1976), however, found that in laboratory colonies of *Ac. octospinosus* and *A. cephalotes*, adult workers, which can feed only on liquids, ingested sap directly from fresh leaves both as they cut fragments and as they prepared the fragments for incorporation into their fungus gardens. Stradling (1978) found that *A. cephalotes* workers ingested liquids while foraging in the field as well. Quinlan and Cherrett (1979) estimated that for a laboratory colony of *A. cephalotes*, the ants' fungus supplied all of the energetic needs of the growing larvae, but only about 5% of needs of the adult workers, with plant sap supplying the remainder. Plant sap collected while cutting fresh leaves is now considered the main carbohydrate source for adult leaf-cutting ants in general (Howard 1991). *Acromyrmex versicolor* foragers, however, harvest no fresh plant material for much of the year (62.5% of samples in the present study). During these times, adult ants must depend on some other source of carbohydrates. This problem is compounded by the inability of adult ants to consume foods except in liquid form. The same problem appears to face *A. mexicana* and most lesser attines.

It is possible that adult attine ants that cut little or no fresh vegetation depend on their fungus for carbohydrates and liquids or the ants may rehydrate dry material within the nest and feed on the sap. Alternatively, these attines may regularly obtain nutritious liquids from other sources such as fruit (Leal and Oliveira 1998), fresh leaves that they do not retrieve, and floral and extrafloral nectaries. Although many ant species commonly feed on the sugary exudate of Homoptera and

Lepidoptera, we know of no records of attine ants using these sources of carbohydrates and water.

Our observation of *Ac. versicolor* foragers at cactus extrafloral nectaries indicates that nectar serves as a source of both carbohydrates and water for these desert leaf-cutters. Further study is needed to evaluate the importance of nectar for desert leaf-cutters. Rico-Gray *et al.* (1998a, 1998b) noted *Atta* feeding on flower nectar at two semiarid sites in Mexico: *Atta texana* in a highland area and an unidentified *Atta* species in a coastal area.

Several studies have recorded lesser attine ants feeding on fluids other than plant sap. Hespeneheide (1985) observed a *Cyphomyrmex* species in Costa Rica visiting extrafloral nectaries on *Byttneria aculeata* plants. Smith and Stark (1989) found an *Apterostigma* species visiting extrafloral nectaries on *Inga* trees in a Costa Rican rainforest, and Tennant (1989) found the same *Apterostigma* species plus a *Cyphomyrmex* species coming to sugar and nectar baits. Koptur (1992) documented *Cyphomyrmex rimosus* workers coming to honey bait in Florida. Murakami and Higashi (1997) found foraging *C. rimosus* workers in Panama often had their crops filled with liquid, and that in *C. rimosus* and *Myrmicocrypta ednaella* workers in laboratory colonies consumed nectar and plant sap.

### **Forager and load size**

Mean forager size in *Ac. versicolor* was intermediate between *Acromyrmex coronatus* and *Acromyrmex octospinosus*, though range of forager size was almost identical to that of *Ac. coronatus* (Table 5). Average burden size was lower for *Ac. versicolor* than for any other species of leaf-cutting ant (Table 5). This difference probably relates in part to the dried nature of most loads collected. Wetterer (1990) found that *A. cephalotes* foragers collecting dried leaf material carried lighter loads than those cutting fresh leaves. In addition, most of the leaves that *Ac. versicolor* harvested come from desert plants with tiny "microphyllous" leaflets.

Mean forager size and forager size-range varied considerably among the different *Ac. versicolor* colonies, between seasons, and even between two collections made five days apart at one colony. The biological significance of this variation is unknown. How the overall size distribution of all workers within *Ac. versicolor* colonies compares to those of other leaf-cutting ant species (Wetterer 1999) also remains unknown.

### **Nesting ecology**

The deep nests of *Ac. versicolor* contrast with the superficial nests of the three *Acromyrmex* species of Central America (see Wetterer 1991,

Table 5. Forager size and load size in *Acromyrmex versicolor* compared with *Acromyrmex coronatus* (Wetterer 1995), *Acromyrmex octospinosus* (Wetterer 1991), *Acromyrmex volcanus* (Wetterer 1993), and *Atta cephalotes* (Wetterer 1994). Symbols as in Table 3. Sample sizes as in Table 4.

Species	$\bar{m}_A \pm 1 \text{ SD}$	range	$\bar{B} \pm 1 \text{ SD}$	$\log m_L$ regression	$R^2$
<i>Ac. versicolor</i>	$5.3 \pm 1.8$	0.8 -10.6	$0.9 \pm 1.3$	$-0.1 + 0.8 \log m_A$	0.07
<i>Ac. coronatus</i>	$3.4 \pm 1.4$	0.9 - 9.0	$1.5 \pm 1.2$	$0.1 + 0.8 \log m_A$	0.18
<i>Ac. octospinosus</i>	$13.3 \pm 4.2$	4.0 -21.2	$1.4 \pm 1.2$	$-0.5 + 1.4 \log m_A$	0.16
<i>Ac. volcanus</i>	$30.6 \pm 4.3$	19.1 -41.5	$1.2 \pm 1.0$	$-1.3 + 1.9 \log m_A$	0.08
<i>A. cephalotes</i>	$7.3 \pm 4.1$	1.4 -32.1	$3.0 \pm 1.4$	$0.6 + 0.8 \log m_A$	0.40

1993, 1995). *Atta mexicana* also has very deep nests (Mintzer 1979). Deep nests in the desert ants appear to be an adaptation for conserving moisture and minimizing daily and seasonal temperature change.

In the present study, most if not all *Ac. versicolor* colonies occurred in areas with greater water supplies relative to the surrounding areas. Wheeler (1907) noted that *Ac. versicolor* colonies typically nest at the bottom of arroyos where the soil was probably somewhat moist at a depth of several feet." Mintzer (1994) noted that *A. mexicana* colonies in an Arizona desert most commonly occur on the banks of large arroyos, areas where much water is stored in the sediments (Atchley *et al.* 1999). *Atta texana* in Texas "prefers the neighborhood of rivers and creeks," typically nesting in the banks (Wheeler 1907). Rockwood (1973) noted that *A. colombica* in a tropical dry forest nested only in riparian forests.

Leaf-cutters in arid habitats may prefer nesting in wetter portions because of the presence of favored plant species (Mintzer 1994) and more common and reliable flushes of fresh leaves and flowers. Lightfoot and Whitford (1991) found that creosote (*Larrea tridentata*) growing along highways had more flowers, higher leaf nitrogen, and lower leaf resin than plants away from the highway and suggested that this may be due to increased water availability. Alternatively, leaf-cutters may use alternative sources of water that are more common in wetter areas.

### Future studies

Many ecological and evolutionary questions remain concerning *Ac. versicolor*, *A. mexicana*, and other desert attine ants. The majority of work on attines has concerned only a few species of tropical leaf-cutting ants, particularly *Atta sexdens*, *A. cephalotes*, and *Ac. octospinosus*. These three species, however, represent only a small fraction of the phylogenetic and ecological diversity of attines. Information on most other attine species, particularly lesser attines, remains largely anecdotal. Detailed comparative studies, which include these neglected

species, put in a phylogenetic context (Schultz and Meier 1995; Wetterer 1999), are needed to understand better the ecology and evolution of this fascinating and important group of ants.

### ACKNOWLEDGMENTS

We thank A. Wetterer, M. Wetterer, B. Sullender, A. Mintzer, and G. Gamboa for comments on this manuscript; M. Pitts, W. Harris, and N. Majer for logistic and administrative assistance; everyone at Biosphere 2 Center, particularly M. Pitts, A. Southern, and A. Holmes for their hospitality and friendship; P. Teal for field assistance; T. McConnaughay and R. Himler for letting us study ants on their property; S. Prchal for his hospitality and for allowing us to work on the property of the Sonoran Arthropod Studies Institute. Financial support was provided by the Center for Environmental Research and Conservation, Columbia University, Biosphere 2 Center, and Florida Atlantic University.

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