pauletia exhibited markedly differing feeding behaviors. *Phyllostornus discol*[illegible] visited high flowers, grasping the branch beneath the flower and pulling [illegible] down. *Glossophaga soricina* visited both high and low flowers and hovered as [illegible] fed. Both bat species aided in cross-pollinating *Bauhinia* (Heithaus et al. 1974

Nectar-feeding bats tend to have large eyes and relatively good vision. They visually locate white flowers that show up well in the dark. The sonar of nectar-feeders is often quite reduced, but the olfactory sense is well developed. Sight and scent, not sound, are how the animals find their sugary dinners. They also have long muzzles and weak teeth, both advantageous in probing deeply into flowers. Finally, they have long tongues covered with fleshy bristles that can extend well into the flower, and their neck hairs project forward, acting as a "pollen scoop." When nectar-feeding bats feed, they pick up a great deal of pollen.

The pollen from bat plants tends to be significantly higher in protein than in non-bat-pollinated plants, and bats ingest pollen as well as sugary nectar. Pollen contains the amino acids proline and tyrosine, useless to the plant but important to the bats. Proline is necessary to make connective tissue such as is used in wing and tail membranes, and tyrosine is essential to milk production. Bats are not the only animals to eat and derive important protein from pollen. Heliconius butterflies (chapter 6) collect pollen on a small brush near their mouth parts, ingesting it after dissolving it with nectar.

Once ingested, nectar helps dissolve the tough pollen coat, but bats aid this process because their stomachs secrete extraordinarily large amounts of hydrochloric acid. These bats also drink their own urine, which helps dissolve the pollen coat, liberating the essential protein. Nectar-feeding bats and bat-pollinated plants, like the figs and fig wasps, are evolutionarily locked together in a mutualistic relationship in which each party is essential to the other.

Ants and Ant-Plants

Figure 89

Some tropical plant species possess nectar-secreting glands as well as other structures that collectively act to attract ants. Indeed, a diversity of plant species ranging through nineteen families (and including ferns, epiphytes, vines and trees) have been classified as "ant-plants" or *myrmecophytes* because of their ant-attractant properties (Benson 1985). Various ant-plants also occur in the Old World tropics, especially Southeast Asia. Ant-plants usually have some kind of shelter for ants (ant domatia) as well as some form of nutrition for them.

Domatia range from mere hollow stems to more sophisticated shelters such as specialized pouches or thorns. Food glands, termed *extrafloral nectaries*, are found on leafblades, leaf petioles, stems, or other locations on the plant. These glands manufacture various energy-rich sugary compounds as well as certain amino acids. In addition, some plants have bead bodies, which are modified hairs rich in oil (Benson 1985).

The odd sugar- and oil-producing bodies initially puzzled botanists, who could identify no obvious function for them. It was soon observed, however that many of the plants with extrafloral nectaries are liberally populated by various ant species, many of which are aggressive. Perhaps the ants, by their

...essiveness, somehow protect the plants, which repay the ants in nectar and ...er. This hypothesis, rather startling at the time, was termed the *protectionist ...hesis,* and it envisioned the relationship between the plants and ants as ...ualistic. The alternative idea, called the *exploitationist hypothesis,* argued ... the ants merely fed on the sugary nectaries but provided no actual service ...he plants. An early (1910) description of the exploitationist hypothesis ...gested that the plants "have no more use of their ants than dogs do their ...s" (quoted in Bentley 1977).

...ecropias are among the most common plants with extrafloral nectaries ... bead bodies. Cecropia nectaries are termed *Mullerian bodies* and are lo...ed at the base of the leaf petiole, where the large leaf attaches to the stem. ...s of the genus *Azteca* live in domatia within modified hollow pith of the ...m and feed on the Mullerian and bead bodies. I have frequently encoun...ed these ants, and they are not nice ants. Cutting cecropias for use as net ...es (to catch and band birds), I have been attacked vigorously by Aztec ants, ...d I have little sympathy for the exploitationist hypothesis. The ants of a ce...pia are pugnacious and thus protective of their tree. If I were a cecropia, I'd ...nt some of these ants living on me. Cecropia have additional structural ...operties that suggest a coevolution with Aztec ants. The underside of the ...de, palmate leaves is velvetlike, with a carpet of tiny hairs and hooks that ...ow ants to gain purchase and so move easily across the leaf. Cecropia species ...at are not mutualistic with Aztec ants have leaves with smooth undersides ...Benson 1985).

Janzen (1966) settled the controversy at least for one ant species. Janzen ...udied *Pseudomyrmex ferruginea,* which occurs on five species of *Acacia* tree. ...ommonly called the bull's horn acacia, the tree has pairs of large hollow ...orns on its stem that serve as homes for the ants. A single queen ant burrows ...to a thorn of a sapling acacia to begin a colony that can increase to as many ...s 12,000 ants by the time the tree is mature. Janzen noted that by the time the ...ast-growing tree was seven months old, 150 worker ants were "patrolling" the ...tem. The acacia ants attack any insects that land or climb on the tree, includ...ng beetles, bugs, caterpillars, and other ants. Ants also clip plants that begin ...o grow nearby or overtop and shade the acacia (thus taking its sunlight), and ...hey attack cattle or people if they brush against the tree. Ants become very ...ctive, swarming out of the thorns and over the foliage even if merely exposed ...o the odor of cattle or people. I was once attacked on the neck by a single ...acacia ant, and the formic acid irritated me for over a day. I can well imag...ne the discomfort that would have occurred if I had been stung by many of ...hese ants.

Why do ants live on acacias? They obtain shelter within the thorns, but they also obtain nutrition from two kinds of extrafloral nectaries. One type is termed *Beltian bodies,* which are small orange globules growing from the tips of the leaflets of the compound leaves, and the other type is called *foliar nectaries,* located on the petioles.

Janzen performed a field experiment that discriminated between the protectionist and exploitationist hypotheses. He treated some acacias with the insecticide parathion, and he also clipped thorns to remove all ants from the treated trees. The antless trees did not survive nearly as well as control trees, which were permitted to keep their ants. Janzen estimated that antless acacias were not likely to survive beyond one year, either falling prey to herbivores or being overtopped by other, competing species of plants. Ants are needed to attack herbivores and clip other plants. An antless acacia is doomed. Janzen concluded that the ants and acacias are obligate symbionts, depending entirely upon each other. The protectionist hypothesis is correct, and an impressive mutualism has coevolved between acacias and *Pseudomyrmex.*

Though both *Azteca* and *Pseudomyrmex* are aggressive ants, many ant plants harbor less obviously aggressive species. However, these more docile ants may nonetheless protect the plant by eating tiny mites or insect eggs (Benson 1985).

Ant-plants may obtain more than just protection from ants. Some may benefit by securing nutrient-rich substrate as a byproduct of ant colony construction and refuse. For example, some epiphytes are known to grow only on ant nests (Benson 1985).

Extrafloral nectaries occur also on temperate zone plants (Keeler 1980) but seem more abundantly represented among tropical species (Oliveira and Leitao-Filho 1987). In a survey of riparian and dry forests in Costa Rica, plants with extrafloral nectaries ranged in percentage cover from 10 to 80% (Bentley 1976). In the Brazilian cerrado, cover by woody plants with extrafloral nectaries ranged from 7.6 to 20.3% (Oliveira and Leitao-Filho 1987). Many plants with extrafloral nectaries house ants, but the degree to which they protect their hosts varies (Bentley 1976, 1977).

But It Can Get Complicated

Extrafloral nectaries, at least in some cases, undoubtedly function as effective bribes from plants to ants, the plant "buying" protection from the ants. But if ant protection can be bought, why not, in an evolutionary sense, sell to the highest bidder? Apparently a few species of lepidopterans from the families Riodinidae and Lycaenidae have discovered this basic tenet of economics. In a remarkable example documented in Panama by DeVries (1990, 1992) and DeVries and Baker (1989), caterpillars of the butterfly *Thisbe irenea* entice ants to protect them, rather than the ants' host plant (*Croton*), and then the rapacious caterpillars eat the leaves from the very plant the ants were once protecting! These caterpillars, termed *myrmecophilous* for their "ant-loving" habits. have evolved at least three separate organs that act to attract and satisfy ants: nectary organs that produce protein-rich ant food; unique tentacles that release chemicals mimicking those of the ants themselves and signaling them to defend; and vibratory papilla, which, when the caterpillar moves its head vigorously, make sounds that travel only through solid objects, but which immediately attract ants. Ants apparently have a much stronger preference for protein-rich caterpillar nectar droplets than for the carbohydrate-rich *Croton* nectaries (why settle for a sugary soda when you can have a burger?), and the ants are essential in protecting the otherwise vulnerable caterpillars from marauding predatory wasps. Thus, by "bribing" the ants, the caterpillars have succeeded in both averting the main protective adaptation of the plant and ensuring their own relative safety from their major predators, wasps.

Fungus Gardens and Leafcutting Ants

Figures 90, 91, 92

No one can visit the Neotropics without encountering leafcutting ants. Throughout rainforests, successional fields, and savannas, well-worn narrow trails are traversed by legions of ants of the genera *Acromyrmex* and *Atta* as they travel to and from their underground cities, bearing freshly clipped leaves. Their trails take them up into trees, shrubs, and vines where they neatly clip off rounded pieces of leaves, which they carry back to their colony. The ants live in underground colonies of up to eight million individuals, consisting of a single large queen and myriad worker ants, most of which remain subterranean. Workers are of several size classes: very small (minimas), medium-sized (medias), and large (maximas). Soldiers, the principal defense class, are large and well armed with formidable pincer jaws. You'll meet them if you dig into a colony. *Atta* colonies are underground, but the bare mounds of soil that mark their multiple entrances spread widely and obviously on the surface. These abundant ants make no secret of their presence. The sight of thousands of leafcutters marching along, most of which are bearing neatly clipped leaf fragments, is unique to the Neotropics. Leafcutters are not to be found in the Old World tropics.

The impact of leafcutting ants may prove enormous. On Barro Colorado Island in Panama, leafcutter ants have been estimated to consume 0.3 ton of foliage per hectare per year, equal to the combined effects of all vertebrates in the forest (Leigh and Windsor 1982). Indeed, estimates suggest that somewhere between 15 and 20% of net primary productivity within a rainforest is consumed by the leafcutters, and the ants may have a devastating effect on local agriculture. Leafcutters are generally selective as to which species they clip (Wetterer 1994). For example, in Guanacaste, Costa Rica, one *Atta* species clipped mature leaves from only 31.4% of the plant species available. Another species used leaves from only 22% of the available plant species, indicating a strong selectivity of both leafcutter species (Rockwood 1976). The commonness or rareness of a plant species has no correlation with *Atta* preference. The ants often travel far from their nest to seek out a certain plant species. Rockwood hypothesized that internal plant chemistry strongly influences *Atta* diet, a suggestion borne out by subsequent research (Hubbell et al. 1984). Ants seem to concentrate on plants with minimal amounts of defense compounds in their leaves (see chapter 6).

Leafcutter ants are part of a larger ant group called the fungus garden ants (Myrmicinae: Attini), each of which, remarkably, cultivates a particular species of symbiotic fungus that makes up its principal food source (see below). Some fungus/ant relationships may be as old as 50 million years. There are approximately 200 fungus garden species, of which 37 are leafcutters. The remaining species, most of which are inconspicuous, cultivate their fungus on some combination of decaying plant or animal organic matter (Holldobler and Wilson 1990). Though most abundant in the tropics, fungus garden ants also occur in warm temperate and subtropical grasslands. One enterprising species even occurs as far north as the New Jersey pine barrens (Wilson 1971).

Leafcutting ants taste and may ingest the sap of the leaves they cut, perhaps using the sap as an additional food source (Wetterer 1994). They do not, however, consume any leaves but rather clip and carry leaf fragments to their colonies. There they use the leaves to make media to culture a specific fungus. This odd fungus, which is never found free-living outside fungus garden ant colonies, is the ants' only food. Leaves brought to the colony are clipped into small pieces and chewed into a soft pulp. Before placing the pulpy mass on the fungus bed, a worker ant holds it to its abdomen and defecates a fecal droplet of liquid on it. The chewed leaf is then added to the fungus-growing bed and small fungal tufts are placed atop it. Other ants sometimes add their fecal droplets to the newly established culture. Detailed photographs from inside an *Atta* colony can be seen in Moffett (1995b).

Worker ants collecting leaves avoid those that contain chemicals potentially toxic to the fungus (Hubbell et al. 1984). One tree, *Hymenaea courbaril*, a legume, has been shown to contain terpenoid (see chapter 6), which is antifungal (Hubbell et al. 1983). *Atta* ants must obviously avoid clipping leaves from this species. The tree has evolved a protection from *Atta*, not by poisoning the ant, but by poisoning its fungus!

The relationship between ants and fungus is unique. The ants culture only a few fungal species, all of which are members of one group, the Basidiomycetes (family Lepiotaceae), a group whose free living members include the familiar parasol mushrooms. The fungi are always in pure culture, protected from contamination from other fungal species by constant "weeding" by ants. Without the attention of the ants, the fungus is quickly overtaken by other fungal species. Both ants and fungi are totally interdependent, an example of a complete obligatory mutualism (Weber 1972). Ant and fungus are inextricably linked by evolution: only the queen reproduces, and when a queen ant founds a new colony she takes some of the precious fungus with her inside her mouth. Fungus and ants disperse together.

Detailed studies of the fungus-ant relationship at the biochemical level has revealed the multiple roles that ants play in culturing the fungus (Martin 1970). The ants clean the leaves as they chew them to make the culture bed pure. Ant rectal fluid contains ammonia, allantoic acid, the enzyme allantoin, and all twenty-one common amino acids. These compounds are all low molecular weight nitrogen sources, and they are the key ingredients in making the culture optimal for the fungus. The fungus lacks certain enzymes that break down large proteins (all of which are made up of chains of amino acids). Thus it depends totally on the ant rectal fluid to supply its amino acids. Experiments attempting to grow the fungus in a rich protein medium failed. It can only grow in a medium of small polypeptides and amino acids. Ants also supply enzymes necessary to aid in breaking down protein chains.

Martin (1970) summarized the functions of the ants as (1) fungal dispersal, (2) planting of the fungus, (3) tending the fungus to protect it from competing species, (4) supplying nitrogen in the form of amino acids, and (5) supplying enzymes to help generate additional nitrogen from the plant medium.

The fungus garden ants are the expert gardeners of the insect world, and their labors pay off handsomely. The fungus symbiont digests cellulose, an energy-rich compound that ants cannot digest. Not only that, but the fungus is unaffected by many, if not most, of the defense compounds contained within leaves of many plant species (see chapter 6). By eating the nutritionally rich fungi, ants circumvent the numerous and diverse defense compounds typical of Neotropical plants, while at the same time tapping into the immense abundance of energy in rainforest leaves. Fungus garden ants owe their remarkable abundance to their unique evolutionary association with fungi.

How such a sophisticated and apparently ancient evolutionary relationship began is difficult to know, but one possibility is that the ant-fungus relationship was initiated simply through predation by ants on fungus. What began as predation evolved over the millennia into mutualism.

Some suggestion has been made that mutualistic associations such as is typified between ants and fungus represent a clear example of how nature can be cooperative rather than competitive, a kind of anti-Darwinian view of nature. But cooperation, however real, is not at all contrary to predictions of natural selection theory. Any obligate or faculative mutualism can just as easily be described as mutual or reciprocal parasitism, where one party is exploiting the other and being exploited in return (though to the ultimate benefit of each). Each party in the mutualism acted and continues to act as a selection pressure on the other. There is nothing anti-Darwinian about that.

For more on the intricacies of coevolution, see Futuyma and Slatkin 1983. For more on ants of all sorts, see Holldobler and Wilson 1990.

The Importance of Fruit in the Tropics

Fruit is both abundant and (relatively) constantly available throughout the year in the Neotropics, making it an important resource for birds, mammals, certain reptiles, occasional fish (chapter 8), and all manner of arthropods (Levey et al. 1994). Where can you go to see a spider monkey, a spangled cotinga, and a common iguana, all in the same tree? Try a fig tree, when it has mature figs. Many Neotropical animals are considered to be *frugivores*, creatures whose diet includes more than 50% fruit (Levey et al. 1994).

In the temperate zone, fruit is a distinctly seasonal resource, occurring from midsummer through autumn. Many birds migrating to winter in the tropics feed heavily on fruit in the fall, but, because fruit is ephemeral in the temperate zone, no bird families have specialized as frugivores (Stiles 1980, 1984). In the tropics, entire families of birds, such as the manakins, cotingas, toucans, parrots, and tanagers, depend heavily on fruit, and some species are almost exclusively frugivores (Snow 1976; Moermond and Denslow 1985). In addition, mammals ranging from bats to agoutis to many monkey species utilize fruit as a major component of their diets. Fruits provide a calorically rich, nontoxic, and easily acquired resource. But there are downsides to a diet of fruit. Protein is usually sadly lacking, thus an all-fruit diet, while rich in calories, is typically nutritionally deficient. Also, fruiting patterns vary, often significantly, in both time and space. In other words, two fruiting fig trees may be widely separated, necessitating searching by frugivorous animals. For example, the great green macaw (*Ara ambigua*), a large parrot species, must make extensive, irregular movements throughout its range in Costa Rica, searching for satisfactory fruiting plants (Loiselle and Blake 1992). Seasonal changes in