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COEVOLUTION OF MUTUALISM BETWEEN ANTS AND ACACIAS IN CENTRAL AMERICA¹

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The purpose of this paper is to discuss the coevolution of one of the more thoroughly studied mutualistic systems in the New World tropics: the interdependency between the swollen-thorn acacias and their ant inhabitants. This system has recently been described in detail in respect to one species of plant, *Acacia cornigera* L. (Mimosoideae; Leguminosae), and one species of ant, *Pseudomyrmex ferruginea* F. Smith (Pseudomyrmecinae; Formicidae), and shown experimentally to be a case of mutualism (Janzen, 1966a). In this species pair, the ant is dependent upon the acacia for food and domicile, and the acacia is dependent upon the ant for protection from phytophagous insects and neighboring plants. The literature

dealing only with the New World tropical acacias (*Acacia* spp.) and their ants (*Pseudomyrmex* spp.) has been re-evaluated by Janzen (1966a) and will not be discussed further in a review sense.

The higher plants that commonly have ant colonies living in them have long been termed myrmecophytes. Ants living in plants range in habit from fortuitous usage of a plant cavity to highly complex interaction systems between the ant and the higher plant. The ant-acacia system represents this latter extreme, and the acacia is by any definition a myrmecophyte. A review paper on the subject of myrmecophytes is in preparation. In the present paper, plants with ants living in them will be called "ant-plants"; the ants will be called "plant-ants."

The "swollen-thorn acacias" are those with 1) enlarged stipular thorns normally tenanted by ants, 2) enlarged foliar nectaries, 3) modified leaflet tips called Beltian bodies (eaten by the ants), and 4) nearly year-round leaf production and maintenance even in areas with a distinct dry season (Fig. 1). Swollen-thorn acacias have been shown experimentally to have a virtually obligate dependency on

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the obligate acacia-ants in lowland eastern Mexico, and are very likely to have a similar relationship in lowland areas throughout Central America (based on field observations). Most members of the genus *Acacia* have no such obligatory dependence on ants, though minor interactions may occur (ant-nectary associations). While the colonies of many species of ants live occasionally in the thorns of swollen-thorn acacias, only those which have colonies solely in swollen-thorn acacias are termed "obligate acacia-ants." In the New World tropics, all of these are in the genus *Pseudomyrmex*; however, most *Pseudomyrmex* do not have an obligate interaction with any living plant, even though they customarily live in hollow branches. The obligate acacia-ants are not specific to any one species of swollen-thorn acacia, but rather to the swollen-thorn acacia life form.

In the literature, swollen-thorn acacias are referred to by various common names (Janzen, 1966b), the most frequent of which is "bull's-horn acacia"; this name is most appropriate for *Acacia cornigera* (Fig. 1b, 1e). Obligate acacia-ants are commonly referred to as "acacia-ants"; unfortunately this name has also been used for various species, usually in genera other than *Pseudomyrmex*, that occasionally live in unoccupied swollen-thorn acacia thorns.

It should be made abundantly clear that the success or failure of any study of a group of tropical plants and insects weighs heavily on the reliability of the identifications, and the degree of correlation between scientific specific names on the one hand, and actual genetically continuous populations on the other. Much

effort to date has been expended in attempts at verification of this correlation by extensive field collection to determine population boundaries, and by close examination of the morphological and behavioral characteristics of the specimens. This portion of the study is still in progress, but it is unlikely that further findings will change the conclusions reached in this paper.

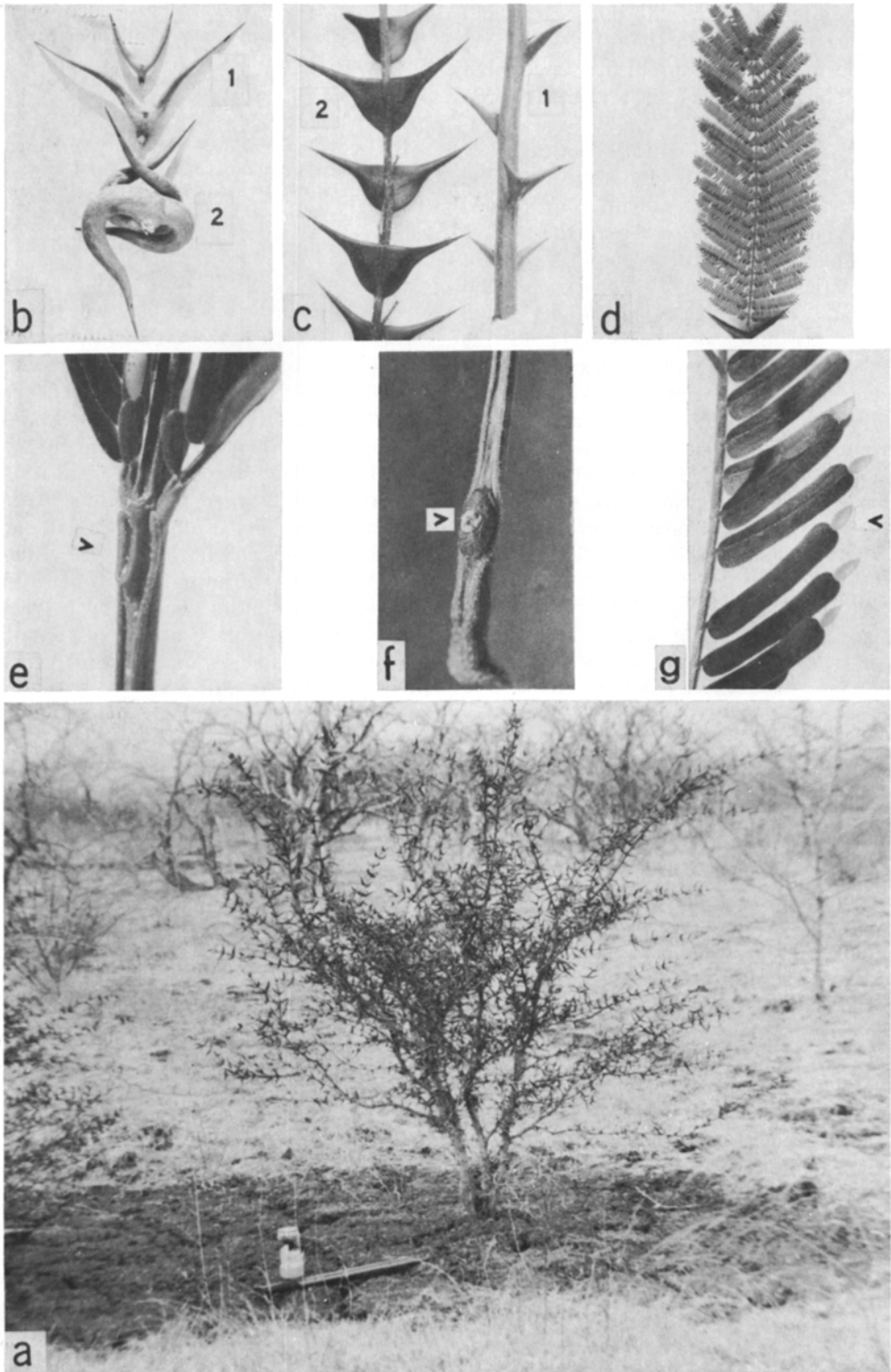
Obligate Acacia-ants

Of the seven large ant subfamilies (family Formicidae), the pantropical subfamily Pseudomyrmecinae is one of the smallest. It contains four genera: *Pseudomyrmex*, New World tropics, 150-plus species; *Tetraponera*, Old World tropics, 100-plus species; *Pachysima* (two species) and *Viticolica* (one species), Congo. Morphologically and ecologically the subfamily is very uniform, and contains many examples of parallelism and convergence, especially in respect to ant-plant interactions. In general behavior and appearance, pseudomyrmecine ants are most similar to the primitive ant subfamily Ponerinae yet at the species level they exhibit some very complex interactions with the environment.

The obligate acacia-ants (*Pseudomyrmex* spp.) are not the only Pseudomyrmecinae associated with living plants. Within the genus *Pseudomyrmex*, there are other species associated with living plants of the genera *Triplaris* (Polygonaceae), *Tachigalia* (Leguminosae), *Cordia* (Boraginaceae), and *Ateleia* (Leguminosae). While it appears that various sorts of interdependencies may exist, these are not included in the present paper. There are no *Pseudomyrmex* species that obliga-

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FIG. 1. a. *Acacia collinsii* in a heavily grazed pasture in southwestern Nicaragua. Note bare basal circle cleared of vegetation by *Pseudomyrmex nigrocincta*. b. *Acacia cornigera* type A (1) and type B (2) thorns; same tree, Veracruz, Mexico. c. *Acacia hindsii* type Z (1) and type B (2) thorns; same tree, Nayarit, Mexico. d. Leaf of *Acacia hindsii*, same tree as c. e. Raised petiolar nectary of *Acacia cornigera*; greenhouse seedling, seed from Guanacaste, Costa Rica. f. Raised petiolar nectary of *Acacia cornigera*; greenhouse seedling, seed from Guanacaste, Costa Rica. g. Beltian bodies on tips of pinules of *Acacia cornigera*, same seedling as f.



torily interact both with an acacia and another genus of plants.

The taxonomic problems associated with obligate acacia-ants are discussed in Janzen (1966c). These ants are essentially restricted to Central America below elevations of 1000 to 1500 meters. Due to the difficulty in identifying pinned specimens of *Pseudomyrmex*, there have been many misidentifications in studies of interactions between *Pseudomyrmex* and *Acacia*. The obligate acacia-ants listed below are discussed collectively in the present paper and possess seemingly taxonomically valid names. *Pseudomyrmex nigropilosa* is an obligate acacia-ant, but is not further considered because it plays no known protective role in the interaction. There are at least three undescribed species not listed below.

Pseudomyrmex ferruginea F. Smith—Tampico, Mexico, south to Acapulco and Merida, Mexico, and thence south to central Guatemala.

Pseudomyrmex belti Emery—western Mexico south to San Jose, Costa Rica on both sides of Central America.

Pseudomyrmex spinicola Emery—central Guatemala south to northern Colombia.

Pseudomyrmex nigrocincta Emery—Tamazunchale, Mexico south to Guanacaste, Costa Rica.

Pseudomyrmex satanica Wheeler—northeastern Panama.

Pseudomyrmex nigropilosa Emery—western Mexico south to Guanacaste, Costa Rica.

Swollen-thorn Acacias

The genus *Acacia* (Mimosoideae), with over 700 nominal species, is distributed throughout the drier portions of the tropics and subtropics. The swollen-thorn acacias as here discussed are restricted to the New World and comprise less than 10 per cent of the genus *Acacia* in Central America (Janzen, 1966b). It appears that swollen-thorn acacias do not extend south past Venezuela or Colombia.

A list of the swollen-thorn acacias discussed in the present paper follows. Two additional species are undescribed and not listed. See Rudd (1964) and Janzen (1966b) for additional taxonomic discussions.

Acacia cornigera L.—Tamaulipas, Mexico, south along both sides of Central America to Guanacaste, Costa Rica.

Acacia sphaerocephala Schlect. & Cham.—isolated pockets from Tampico south to Yucatan, Mexico.

Acacia hindsii Benth.—Mazatlan, Mexico, south to Honduras, thence up the Caribbean to Guatemala.

Acacia collinsii Stafford—Tehuantepec, Mexico, south along the Pacific slope to Colombia, some extensions into eastern Guatemala and Honduras.

Acacia melanoceras Beurling—northeastern Panama.

Ant × Acacia Interaction

The basic interaction between *Acacia cornigera* and *Pseudomyrmex ferruginea* in lowland eastern Mexico is representative of a fully developed interdependency. The queen ant finds an unoccupied seedling or sucker shoot of the acacia by flying and running through the vegetation. "Unoccupied" as used here, refers to the absence of workers of obligate acacia-ants outside of the swollen thorns. She either cuts her own entrance hole in a green swollen thorn or uses one cut by a previous worker or queen. She lays her eggs in the thorn and forages out of it for nectar from the foliar nectaries (Fig. 1e, 1f) for herself and larvae, and solid food (Belgian bodies; Fig. 1g) for the larvae. As the colony grows, it occupies all of the thorns of the plant, with up to 25 per cent of the workers normally active at any one time outside of the thorns, but on the acacia. By this time the queen's abdomen has become greatly enlarged (physogastric) and the workers fulfill all of the working, foraging, and protective functions in the colony. About nine months of colony growth are necessary to produce enough old workers to patrol the outside of the acacia in an effective and aggressive manner. By the time the colony contains about 1200 workers, the first winged reproductives are produced, and alate production is thenceforth continuous except under conditions of severe starvation. Colonies may grow to contain as many as 16,000 workers in three years, or 30,000 after an indefinite period. During this colony expansion, the colony often moves out to inhabit neighboring acacias (auxiliary-shoots) within three to 10

meters, but the queen usually stays in the original shoot (queen-shoot). Colonies with over 50 to 150 workers actively patrol the outside of the shoot on a 24-hour basis.

With a few notable exceptions (insects that have evolved mechanisms to feed in the presence of the ants), the workers attack any other insects on the acacia and normally are successful in driving them off by biting and stinging (see Table 6). They also attack (mauling with mandibles) any living foreign plants which touch the swollen-thorn acacia's foliage or grow in an area 10 to 150 cm. in diameter below the acacia (basal circle; Fig. 1a). Thus the acacia grows in a cylindrical space free of other plants. The efficiency of removal of insects and foreign plant parts from the acacia is a function of worker aggression and patrolling consistency, which is in turn a function of colony size, air temperature, and food availability (foliar nectar and Beltian bodies).

The young acacia grows in young second growth, from a seed or from a stump left by fire, flood, or land clearing. As it grows during the first nine to 24 months without being occupied (assuming that a mature colony has not found it and moved into it as an auxiliary-shoot), it is subject to insect and rodent attacks which greatly reduce the already small population of young acacias. During the early stages of growth, a seedling progressively produces larger thorns, more leaflets with Beltian bodies, and larger foliar nectaries until it has these morphological properties of a mature acacia. Once occupied, the acacia grows very rapidly as an emergent or canopy member during the first six to eight years of undisturbed regenerating second-growth vegetation. Several large seed crops are produced during this time. In undisturbed regenerating vegetation, the acacia shoot rarely lives more than eight to 10 years; in open, repeatedly disturbed sites (pastures, roadsides), it may live at least 20 years. Only after a dry season of over five months' duration

is the entire leaf crop dropped without gradual replacement of leaves.

It has been experimentally demonstrated that the swollen-thorn acacia has lost, apparently through evolutionary change, its ability to withstand the phytophagous insect damage and competitive pressure of neighboring plants without the protection of the obligate acacia-ants (Tables 2, 3, 4, and Janzen, 1966a). Unoccupied swollen-thorn acacias show severe defoliation and loss of growing shoot tips. Repeated such losses usually cause death within six to 12 months; moreover, the plant is unable to maintain the high vertical growth rate necessary for a sun-loving plant in tropical lowland second-growth plant communities. The acacia is then heavily shaded by the surrounding growing plants, and the harm is aggravated by the frequent use of the acacia as a support by vines. Even though the acacia may flower as a damage reaction under these circumstances, this does not result in a seed crop inasmuch as it requires about a year to mature the seeds.

The obligate acacia-ant may thus be regarded as a multipurpose characteristic of the acacia, maintained by swollen thorns, Beltian bodies, enlarged foliar nectaries, and year-round leaf production. Evolution of these features is associated with that of various traits of the ant such as aggressiveness towards foreign organisms, use of Beltian bodies as a protein source, etc. The size of the ant colony is a function of the rate and continual nature of leaf production; the thorns, nectaries, and Beltian bodies are all foliar structures.

In the demonstration of the above dependency, ants were experimentally removed from the acacias by either clipping the thorns, or cutting and burning shoots with their ants, and observing unoccupied growth from the stumps. In the experimental subplots, the unoccupied shoots and new suckers grew for at least seven to nine months without ant colonies and were compared with the occupied growth in the control plots. Tables 2, 3, and 4

contain representative data from these experiments. Fifty subplots were under observation for four to 11 months.

Evolutionary System

The system described for *Acacia cornigera* and *Pseudomyrmex ferruginea* differs somewhat from that of other species pairs. Of importance are variations in the type of plant community, aggressiveness of the ant species, size of the colony, and abundance and presence of insects that attack unoccupied acacias. In drier sites and heavily grazed pastures, unoccupied acacias are in little danger of being shaded (e.g., *Acacia collinsii* in southeastern Nicaragua). It is common for two or more species of obligate acacia-ants to occur at the same site; one usually is more efficient at protecting the acacia than the other (e.g., *Pseudomyrmex belti* is less effective than *Pseudomyrmex spinicola* in central Costa Rica). Some species of obligate acacia-ants will accept newly fecundated queens into the colony and thus increase the colony egg production. The resultant large colonies can effectively patrol several hundred acacias (e.g., *Pseudomyrmex belti* in Nayarit, Mexico) while single-queen colonies can rarely effectively patrol over 20 (e.g., *Pseudomyrmex ferruginea* in Veracruz, Mexico). On a local basis, and even more strikingly over the annual cycle from wet to dry seasons, the presence of insects that severely damage unoccupied acacias is quite variable; these insects must be censused in any experiment designed to verify the presence of a mutualistic interaction. While large vertebrate herbivores may have been of importance in the evolution of the interaction (Brown, 1960), they are not the major present-day selective force in its maintenance. During the end of the dry season, when swollen-thorn acacias may be the only green plants available, small rodents (e.g., *Sigmodon hispidus*) may do considerable damage to unoccupied acacias; this damage has the same impact as the generally much more common insect damage.

The traits of the ant and the acacia (Tables 1 and 5) can be roughly divided into two groups: (A) those shared with other species of the genera concerned, and therefore presumably present to some degree in the prototype obligate acacia-ant and swollen-thorn acacia before any interaction existed; and (B) those features in which the mutualistic *Acacia* and *Pseudomyrmex* depart from their congeners. Some group A characteristics may be regarded as preadaptations, while group B is richer in novelty. Group B can be further subdivided into those traits essential for the interaction and those that are made possible by it. While some difficulty is encountered in determining what are "normal" traits for the genera *Pseudomyrmex* and *Acacia*, some 70 species of the former and 20 of the latter have been examined in the same areas where the studies of the ant-acacia interactions were made.

SWOLLEN-THORN ACACIAS

(1.) Acacias usually are shrubs or small trees. Swollen-thorn acacias range from low shrubs to trees up to 30 m. tall with 50 cm. DBH; they have tough and resilient wood. Such a structure is necessary to support the large weight of woody swollen thorns and the emergent acacia canopy. The canopy of a two-meter-tall acacia may carry one kilogram of swollen thorns; a four-meter plant, three kilograms. The lateral branches are often the stiffest for their age in the second-growth vegetation during the first four to six years of succession. Nevertheless, in some cases the weight of thorns becomes too great and the top of the acacia bends over, decreasing the plant's height by as much as a meter. The heaviest thorns on the tree (type B; Fig. 1b2, 1c2) are borne on short lateral branches from mature thorn axils on major branches. It appears that further enlargement of the thorns would require strengthening of the lateral branches.

During the first five to 15 years of undisturbed succession, the occupied and

TABLE 1. *Acacia* traits related to the ant-acacia coevolution.

A. General features of acacias of importance to the interaction	B. Specialized features of swollen-thorn acacias (coevolved traits)
1. Woody shrub or tree life form (Fig. 1a)	1. Woody but with very high growth rate
2. Reproduce from suckers	2. Rapid and year-round sucker production
3. Moderate seedling and sucker mortality	3. Very high unoccupied seedling and sucker mortality
4. Plants of dry areas	4. Plants of moister areas
5. Ecologically widely distributed	5. Ecologically very widely distributed
6. Leaves shed during dry season	**6. Year-round leaf production
7. Shade-intolerant, sometimes covered by vines	7. Shade-intolerant and free of vines
8. Stipules often persistent	**8. Stipules longer persistent, woody with soft pith (Fig. 1b, 1c)
9. Bitter-tasting foliage	9. Bland-tasting foliage
10. Each species with a group of relatively host-specific phytophagous insects, able to feed in the presence of the physical and chemical properties of the acacia	10. Each species with a few host-specific phytophagous insects, able to feed in the presence of the ants
11. Foliar nectaries	**11. Very enlarged foliar nectaries (Fig. 1e, 1f)
12. Compound unmodified leaves (Fig. 1d)	**12. Leaflets with tips modified into Beltian bodies (Fig. 1g)
13. Flowers insect-pollinated, outcrossing	13. Same as A 13
14. Seeds dispersed by water, gravity, and rodents	14. Seeds dispersed by birds
15. Lengthy seed maturation period	15. Same as A 15
16. Not dependent upon another species for survival	16. Dependent upon another species for survival

** Essential to the interaction.

maturing swollen-thorn acacia canopy normally maintains a position in the upper part of the general canopy of emergent to it; this is accomplished by a very high vertical growth rate (as much as 2.5 cm. per day) accompanied by ant protection of the tender shoot tips and ant removal of encroaching vines. It is of interest that the new green shoot tips of swollen-thorn acacias lack the fibrous material which makes the shoot tips of other acacias very tough and resistant to breakage, and presumably resistant to insect feeding; the shoot tips of other acacias grow much more slowly. The caterpillar of *Coxina hadenoides* (Noctuidae) eats shoot tips of swollen-thorn acacias at about three times the rate of other acacias in the area; it chews slower on these tougher structures. In general, high rates of branch elongation tend to be correlated with tender and fragile shoot tips. It is doubtful that the swollen-thorn acacias could maintain their

high rate of vertical growth and a tough insect-resistant shoot tip at the same time. In most of the young lowland second-growth plant communities, the other canopy members and emergents are not in the genus *Acacia*.

(2.) The swollen-thorn acacias regenerate rapidly from cut or burned stumps and from lateral roots; under conditions of man-made disturbance, nearly all acacia shoots are younger than their root stocks. Other species of acacia reproduce readily from root stock, but often fail to produce new suckers from stumps cut during the dry season, until the following rainy season starts; such a pattern would be fatal to the tenant ant colony. Sucker regeneration is important to any woody plant in second growth that is commonly subject to fires during the dry season. When the swollen-thorn acacia shoot is cut or killed by heat from a fire, it must put out new suckers rapidly so that the

ant colony does not starve. If the colony dies or moves to a new acacia, the new sucker shoots will lack protection from the ants for from nine to 15 months. The first suckers appear from one to two weeks after the shoot is killed; the ant colony then moves into new thorns. It is notable that the new suckers have fully developed thorns, nectaries, and Beltian bodies (in contrast to seedlings, which gradually develop these features).

The tenacity of the root system is also important in keeping the young seedling (or sucker) alive long enough for a colony to develop from a founding queen (minimum of seven to nine months), or a mature colony to find the unoccupied acacia. This is reflected in the population's structure. There is a very slow rate of input of entirely new plants into a given area, but maturing plants with an ant colony exhibit a very low mortality rate. During any one-generation cycle, the unoccupied shoots do not reach reproductive maturity and incur moderate to heavy mortality.

(3.) Apparently, most acacias have normal seedling and sucker mortality. However unoccupied seedling and sucker swollen-thorn acacias are subject to very high mortality compared to the occupied swollen-thorn acacias. Once a plant has become occupied by a healthy obligate acacia-ant colony, there is a high probability that it will produce a seed crop except in frequently burned or cut areas; in these areas, almost no seed is produced, and the entire reproduction is through stump suckers and sprouts from lateral roots. Seedlings and suckers have the same extreme susceptibility to insect attack that mature plants have; it takes seven to nine months at a minimum to produce an ant colony from a founding queen, and during this time many of the young plants are eaten. Evolution of more rapid colony production could occur through production of Beltian bodies, nectaries, and swollen thorns at the first node of the seedling or sucker. In the seedling, this does not occur until the 10th to 20th node but the seedling probably

lacks sufficient energy reserves until this time.

(4.) While the swollen-thorn acacias inhabit wetter habitats than most other members of the genus *Acacia*, they still appear to be restricted to areas with a distinct dry season. There is no obvious interaction with other members of the community which makes this restriction necessary. Still, the swollen-thorn acacias maintain a high population density in second-growth plant communities that are in general much wetter (one- to three-month dry season) than those where other acacias are common. This dominance is most immediately associated with their high rate of growth (keeping them in the canopy or above) and their freedom from surrounding vegetation (pruning activities of the obligate acacia-ants), both of which enable them to compete in such rapidly growing vegetation. There appears, however, to be a more direct evolutionary consideration; the shorter the dry season, the less time the swollen-thorn acacia has a reduced leaf output and the faster the ant colony grows. The faster the ant colony reaches maturity, the quicker the acacia becomes relatively free from surrounding plants and phytophagous insects. Thus it appears that there is selective pressure for the swollen-thorn acacias to inhabit the wettest areas possible. At the dry margins of their ranges, the swollen-thorn acacias are generally found only in the wettest sites (ravines, road shoulders, swamps); it is only in these places that they can hold their leaves long enough to keep the ant colonies alive.

(5.) In general, the genus *Acacia* contains plants of second growth or low primary growth in dry areas. The swollen-thorn acacias occur as apparently reproductive populations under a much wider range of rainfall, temperature, soil, and disturbance absolute values and patterns. They are found at sites with a dry season of one to six months' duration, and a mean annual rainfall from 1500 to 4000 mm. They grow in areas with a mean annual temperature of 21° to 30° C., with

monthly means varying from about 14° to 32° C., and a cool season of zero to three months' duration. Within these areas they are found on almost every imaginable type of soil from old lava to laterite, black swamp mud, and new beach sand. They may be found under almost any pattern of disturbance except that of pastures where all woody plants have been grubbed out by hand, annually plowed fields, and areas burned annually for more than three consecutive years. Swollen-thorn acacias are clearly ruderals—plants of disturbed vegetation—and they nearly disappear when there has been more than 20 years of undisturbed regeneration (no cattle, fire, or cutting). In primary forest of dry areas, they are plants of the small natural disturbance sites; they also grow rarely as suppressed seedlings, with an ant colony, for several years until a hole appears in a low canopy. Then the plant shoots up to become a reproductive individual.

(6.) In any given population of swollen-thorn acacias, a large number of the plants have green leaves on them throughout, or nearly throughout, the year. These acacias are characteristically the last plants in young second growth to drop their leaves in an exceptionally dry year. Other members of the genus *Acacia* usually drop their leaves and produce no more leaves during the last three-fourths to one-half of the dry season. On swollen-thorn acacias, there is little vertical growth during the dry season, but leaf production is in the form of small axillary tufts of leaves and leaves on the flower bearing shoots; these small leaves have Beltian bodies and fully developed nectaries, but are not subtended by swollen thorns. The products of these leaves are essential to keep the ant colony from starving to death or migrating to another acacia that has leaves. The acacia needs an ant colony during the dry season for at least three reasons: 1) to protect the new flowering branches; 2) to protect the woody parts of the plant from rodents and ovipositing wood-boring beetles; and 3) to have a healthy colony in occupation

when the rainy season begins. There are two courses of flexibility in the ant's dependency during a severe dry season; a colony can starve for three to five weeks without losing all of its members, and portions of the colony can temporarily move into other acacias occupied by the same colony and that still have leaves.

With respect to completeness and duration of leaf drop during the end of the dry season, there is notable genetic and age variation within a given species of swollen-thorn acacia. Suckers and seedlings less than a year old generally do not drop their leaves at all; this is very significant for the founding queens that need the products of the leaves to stay alive and produce a small colony. Stumps cut or burned during the driest part of the year still put out new suckers immediately, which either enables the old colony to move into them, or a founding queen ant to start a colony promptly. However, seeds do not germinate during the dry season. Some maturing swollen-thorn acacias may hold their leaves and produce new axillary tufts as long as a month after others. When a colony occupies several acacias, its components generally consolidate into the one that holds its leaves longest; this plant generally does better than the others when the rainy season begins because at that time it has a higher worker density. The queen is in this acacia, and her acacia generally has more workers; the workers may take several weeks to a month or more to move back into the acacias abandoned during the dry season. Thus there is obvious selection against leaf drop. That the plants show any periodicity in leaf drop is probably a reflection of a serious physiological disadvantage in holding the leaves during a severe dry season.

(7.) The entire genus *Acacia* in the Central American tropics is shade intolerant; the plants do not achieve reproductive maturity as long as the acacia canopy is in full shade. Leguminosae in general are not plants of shaded understories, but rather are members of the canopy and

second growth. However, occupied swollen-thorn acacias are capable of surviving as shade-stunted seedlings for several years (with thin branches, very small thorns, thin nectar, and few Beltian bodies). Lack of shade tolerance is of great importance to the interaction; when unoccupied swollen-thorn acacias are damaged by insects or covered by vines, they are submerged below the general canopy. The immediate reduction in growth due to shading greatly reduces the acacia's ability to recover from the insect damage, and consequently to recover from the submerged position even if it becomes occupied. Thus it is important that seedlings and suckers in newly cleared sites become occupied quickly; within a year the vegetation is often too heavy or too high for the shaded seedling to grow up through.

In general, other species of acacia are swamped by vines and overtopped by the surrounding upright vegetation when they attempt to grow in the dense second-growth communities where swollen-thorn acacias are so common. In more open communities, such as heavily browsed pastures, unoccupied swollen-thorn acacias are in little danger of being shaded. However, insect damage in these sites is very severe. Emergent unoccupied acacias are especially liable to insect damage and use by vines as standards. Associated with the gap in the vegetation around occupied swollen-thorn acacias, the acacias have leafy branches much closer to the ground than do other general canopy member species in the area. While not due to any direct trait of the occupied swollen-thorn acacia, the acacias are characteristically free of vines and do not have foreign vegetation projecting into the canopy; this is due to the obligate acacia-ants' pruning activities. Unoccupied swollen-thorn acacias make excellent standards for vines, with their stiff upright form, thorny and strong lateral branches, compound leaves, and emergent position. The pruning abilities of the ants have allowed the swollen-thorn acacias to move into the

lush second-growth communities where direct competition by vines is a major factor.

(8.) A large number of the New World acacias have woody stipules of various lengths with sharp tips. As their name implies, the persistent woody stipular spines of swollen-thorn acacias are enlarged in diameter and often in length (Fig. 1b, 1c). If the thorns were not persistent, they would be of little use to the ant as domatia; they stay on the acacia for two to four years but after one to two years they are not accepted as domatia by the ants. The total volume of a thorn ranges from 0.1 to 7.0 cc.; usually a swollen-thorn acacia canopy contains 100 to 800 cc. of internal thorn volume. The entire brood and a large part of the workers in the colony are found in the swollen thorns of the acacia(s) that it occupies. The ants cut an entrance hole through one wall of the thorn near one apex while the thorn is still green but fully expanded. The soft and sweet parenchyma is excavated and dropped from the acacia. The outside of the thorn is waterproof for at least two years; the inside wall is water-absorbent and as such is probably functional in regulating the moisture content of the thorns. Especially during the dry season when insects are scarce, the hard-walled thorns serve to protect the ants from birds; the thorns with thinner walls are sometimes opened and if the queen is not in a heavy-walled thorn, she may be lost with resultant death of the colony.

The evolution of spines as a possible deterrent to browsing vertebrates has received sporadic attention in the literature (see Brown, 1960). It is generally the case that spiny plants, such as many acacias, are often found in dry areas where green plant matter is scarce during parts of the year. Presumably these spiny plants are not absolutely free from browsing pressure, but the spines probably serve to place the plant farther down the vertebrate's host preference list.

It is very easy to postulate that all of

the modifications of the swollen thorns from a "normal" stipular spine were evolved to maintain a larger and more stable obligate acacia-ant colony. This ant colony should then in turn favor the genotype that has better thorns. In the several other species of acacia which have fairly large thorns, obligate acacia-ant queens occasionally try to excavate a cavity; the internal pith is too hard and the thorn wall, even when green, is too tough. It is of obvious advantage to the acacia to have the entire ant colony located in its canopy; in order for this to occur, there must be a substantial volume of domatia on the acacia. The prototype acacias have some thorns that are adequate as domatia, but there are not nearly enough to support an ant colony large enough to patrol the tree. The colony in the swollen-thorn acacia canopy is fully exposed to sunlight, bird predation, rain, and desiccation; the thorn walls must be waterproof and somewhat resistant to sudden increases in temperature. When fires are hot enough to kill the shoot, they often do not kill the ant colony, and later it moves into the new sucker shoots from the root stock. While the swollen thorns have retained their sharp tips throughout this evolution, they do not adequately cover the long leaves (much longer and larger than those of most other acacias) and browsing mammals (cattle, deer) easily pluck the large leaves from unoccupied branches without coming into contact with the thorns (Fig. 1d).

(9.) A striking feature of swollen-thorn acacias is that their foliage does not have the extremely bitter taste, to the author and other humans, that characterizes other members of the genus *Acacia* (at least 12 species sampled in Central America). While the responsible compound in the other acacias has not been identified, such a mild taste in the swollen-thorn acacias is indicative of a lack of some so-called "secondary" plant substance. It is postulated that this bland chemical nature of the swollen-thorn acacia explains in great part why the unoccupied acacia

is so heavily used as a food plant by a large variety of insects that normally feed only on other acacias (see Janzen, 1966a, for a list of these insects). Each of these insects is relatively specific to some other species of acacia, yet the unoccupied swollen-thorn acacia is very much acceptable to all of them. It also appears that though the compounds which normally serve to restrict the insect to other plants are lacking in the swollen-thorn acacia, it still has enough of the chemical properties of the entire genus to be recognized as a host plant by many phytophagous insects.

If it is the case that the swollen-thorn acacias really lack some chemical properties (which are replaced in function by the obligate acacia-ants), then it seems reasonable to postulate that 1) the swollen-thorn acacias have lost these properties because the ants take their place, and 2) these compounds are not mere "incidental" by-products but instead are relatively "expensive" materials which were evolved directly in response to feeding pressure from phytophagous insects. At the present day, it seems unnecessary to implicate browsing vertebrates as a selective force in the production of such compounds in other acacias (due to the ubiquity and importance of browsing insects), but it is definitely the case that unoccupied swollen-thorn acacia foliage is much preferred over that of other acacias by cattle, brocket deer, and small rodents. With the exception of the small rodents, which may kill many small unoccupied shoots during the dry season, modern browsing vertebrates appear to have much less impact on second-growth vegetation than do insects, in the lowland tropical second-growth plant communities under consideration (Janzen, 1966a).

(10.) Most acacia species have a small group of insects that feed specifically on each of them, and a variably larger group of somewhat more general feeders which occasionally attack them. Often the usual feeder on one or two species is an occasional feeder on a variety of other species

TABLE 2. Representative mean length increments of occupied suckers from stumps (subplot A-2) and unoccupied suckers from stumps (subplot A-1) cut on May 25, 1964 (Temascal, Oaxaca, Mexico). Ants removed from subplot A-1 by burning the ant-infested canopies, once removed from the subplot (*Acacia cornigera* × *Pseudomyrmex ferruginea*, Janzen, 1966a).

Sub-plot	Time interval	Occupied stumps/total		Length		Increment	
		Begin	End	\bar{X}_0 (cm)	S.D. ₀ (cm)	\bar{X}_{inc} (cm)	S.D. _{inc} (cm)
A-1	25 May–	0/42	0/42	0.00	0.0	6.23	5.6
A-2	16 June	29/29	26/29	0.00	0.0	30.96	17.1
A-1	16 June–	0/42	1/42	6.23	5.6	10.23	9.8
A-2	3 August	26/29	29/29	30.96	17.1	72.86	37.4

in the subfamily (Mimosoideae). In addition there are the few generalized feeders (mostly Orthoptera and Lepidoptera) in the community that feed on a wide variety of plant families. This complex of insects and acacias has evolved to a continually shifting equilibrium whereby the insects eat enough of the specific plant parts to supply the necessary energy flow into their populations, yet do not eat so much that they have an immediate drastic effect on the host acacia population. The bruchid-acacia seed interaction, discussed in the last section, is an example of such a system. The obligate acacia-ants, inasmuch as they are phytophagous and specific to the swollen-thorn acacias, represent a special case.

As do the other acacias, the swollen-thorn acacias have a small group of phytophagous insects that feed on them. These insects have various morphological and behavioral traits which allow them to feed in the presence of the ants (e.g., 1) impenetrable cuticle coupled with no avoidance reaction to ants—*Pelidnota punctulata*, Scarabaeidae, 2) totally ignored by the ants—*Syssphinx mexicana*, Saturniidae, and 3) throw off the attacking ants—*Coxina hadenoides*, Noctuidae). It can be assumed that the prototype swollen-thorn acacia had a group of insects feeding on it. As the ant × acacia interaction gradually developed, these insects were very likely forced off the acacia. However, this leaves the swollen-thorn acacia as a large food source for any insect that can evolve a mechanism to

feed in the presence of the obligate acacia-ant, an event that has happened in at least nine different species of insects now found only on swollen-thorn acacias (e.g., *Syssphinx mexicana*, Saturniidae; *Pelidnota punctulata*, Scarabaeidae; *Coxina hadenoides*, Noctuidae; *Rosema dentifera*, Notodontidae). There are at least two insects specific to the small, naturally unoccupied seedling and sucker population (*Mozena tomentosa*, Coreidae, and *Aristotelia corallina*, Gelechiidae). They, along with rodents in the dry season, are responsible for much of the mortality of these small unoccupied swollen-thorn acacias.

For swollen-thorn acacias, the obligate acacia-ants may be regarded as replacing in some sense the physical and chemical protective properties of other acacias, and the ants are a multipurpose property at that, since they attempt to remove a very large number of species of insects. That this system is so amenable to study is due to the facility with which the ants can be removed without doing direct damage to the acacia; such things as secondary plant substances and some micromorphological properties cannot be so readily removed or altered, but their significance to the plants not associated with ants appears to be of the same nature as the obligate acacia-ants to the swollen-thorn acacia.

(11.) Raised, nectar-producing glands (nectaries) on the upper side of the leaf petiole and/or rachis are almost universally present on Central American acacias. They are visited by a large assortment of

predaceous and parasitic Hymenoptera, beetles, cockroaches, and flies. The presence of the predaceous and parasitic members of this assortment, and especially the ants, is significant in that they may start their predating activities at the site of the nectar, and then radiate outward; thus it is that the acacia may be the plant that is searched for phytophagous insects first and most thoroughly. It is clear that this removal of phytophagous insects, and especially those that feed on shoot tips, is likely to be an advantage to the acacia. Even if this is not the basis for the original evolution of the nectaries, they have such a function at present and the most extreme examples are in the swollen-thorn acacias with their obligate acacia-ant colonies, which receive virtually all their sugars from the nectaries. It should be noted that the evolution of foliar nectaries should be no more difficult morphologically than floral nectaries, since flowers are believed to be in general modified branches and leaves. In acacias in general, the development of the nectaries has probably evolved to the point where the energy necessary for their production and maintenance about balances with the protective value of the predaceous and parasitic insects.

The foliar nectaries of swollen-thorn acacias (Fig. 1e, 1f) are much larger and have a much heavier nectar flow than those of other acacias examined. This nectar is about the consistency of Karo syrup, and a two-meter acacia produces about 1 cc. per day (40 mg. of glucose and fructose combined). This sugar is virtually the entire sugar source of the obligate acacia-ant colony; it may be slightly augmented by some sugars from the sweet parenchyma in the new green swollen thorns. It is postulated that the evolutionary elaboration of the foliar nectaries was in large part responsible for the gradually increasing attraction of the prototype *Pseudomyrmex* to the prototype swollen-thorn acacia. The acacia provides a large and reliable sugar source to the ant species, and this leads into the more

complex interaction. The nectar production is a critical part of the coevolutionary aspects of the ant \times acacia interaction system; more nectar means more ants and more ants mean more nectar through increased foraging and/or patrolling on the acacia foliage, which in turn leads to more leaf production, which thus leads to more nectar production.

(12.) Acacias frequently have twice-compound leaves with 500 to 2000 leaflets. Only the swollen-thorn acacias, or acacias presumably genetically related to them, have the tips of these leaflets modified into Beltian bodies (Fig. 1g; named after Thomas Belt, the first man to describe the interaction—see Belt, 1874). Beltian bodies are constricted leaflets, pinnae, and rachis ends, and the midvein runs nearly to their tip; they are not glands.

The large thin-walled cells in Beltian bodies are apparently full of cytoplasm and other nutrients of a proteinaceous and fatty nature. They also include vitamins; German cockroaches grow on them nearly as well as they do on a yeast diet. The ants harvest them shortly after they are fully expanded on the new leaves, cut them up, and feed them to the larvae; the adult ants (workers) may receive some nutrients from the fluids released during cutting. The nectar and Beltian bodies constitute virtually all of the food of the obligate acacia-ant colony; only rarely is a small insect caught and parts of it used as food for the larvae.

The Beltian bodies are the most unique botanical part of the interaction; they represent no preadaptation by the swollen-thorn acacia and there are no analogous structures on other legumes. The only clue to their origin lies in an undescribed species of eastern Costa Rican acacia which may be regarded as a prototype; some plants of this species have leaflets with a small, clear apical portion. If any one of the six *Pseudomyrmex* species that lives in the occasional large thorns of this acacia and uses its nectaries were to evolve the trait of harvesting these clear leaflet

TABLE 3. *Total wet weight of suckers regenerated, and leaf crop from occupied stumps (subplot H-3) and unoccupied stumps (subplot H-2); stumps cut on October 17, 1963, regeneration harvested August 5, 1964 (Temascal, Oaxaca, Mexico). Ants removed as in Table 1 (Acacia cornigera × Pseudomyrmex ferruginea, Janzen, 1966a).*

Sub-plot	Number of stumps	Total wet weight, gms.	Total number leaves	Total number swollen thorns
H-2	66	2,900	3,460	2,596
H-3	72	41,750	7,785	7,483

tips to augment their insect food, especially during the early part of the dry season when food becomes very scarce, the system would be started. Such a food supplement would increase the size of the colony and therefore increase the foraging on the surface of the acacia. This should lead to more leaf and flowering branch production, which would in turn lead to more ants, plus selection for increased nutritional quality of the new structure, leading eventually to a fully developed Beltian body. In addition, continuity and density of reproductives from a *Pseudomyrmex* colony is directly proportional to the size of the ant colony; thus selection for use of a new food such as this will be favored.

(13.) It appears that all of the Central American acacias are insect pollinated, and there is no reason to believe that they do not regularly outcross. Moderate outcrossing is of importance to an evolutionary interaction system that is to be sensitive to slight selective differences favoring one genotype over another, and lead to gradual evolution of behavioral and morphological systems favorable to the interaction. The habit of flowering during the end of the dry season, when obligate acacia-ant activities are at their lowest, probably lowers ant interference with the visiting bees. However, most of the bees (Megachilidae, Halictidae, *Trigona*, *Ceratina*) are quite persistent and when chased from one flower, they imme-

diately go to another; this of course promotes outcrossing.

(14.) The swollen-thorn acacias are unusual among Central American acacias in that they have bird-dispersed seeds; the seeds are imbedded in a sweet pulp in an indehiscent or dehiscent pod. This pulp is bright yellow in the dehiscent species. The ants generally attack the visiting birds, but the birds move rapidly enough so that they are not sufficiently bothered to leave. Orioles (*Icterus* spp.) eat large quantities of obligate acacia-ants along with the fruit, but rarely eat the seeds. The most effective distributors are birds of second-growth vegetation (e.g., *Psilorhinus mexicanus*), which then tend to drop the seeds in the same types of habitat where they picked them up. There is high seed mortality from bruchid beetles while the pods are still on the swollen-thorn acacias; it is the birds' activity in eating some seeds before the bruchids oviposit on them that is the primary factor that saves enough seeds to maintain the population. Both in man-made and natural disturbance sites, a relatively high and continuous viable seed input is necessary to produce enough seedlings to get a very few acacias to the stage where they are occupied by obligate acacia-ants; in view of the heavy weight of acacia seeds, birds seem to be the only wide-ranging candidates for such a dispersal agent. Other acacias depend on gravity, water, and rodents for dispersal, and are often very slow to move into newly cleared areas.

(15.) It appears to be a general rule among the woody Central American acacias that the seeds maturing during one dry season are from the flowers pollinated during the preceding dry season. Therefore a swollen-thorn acacia must live six to nine months after it produces flowers in order to contribute seed to the population; flower production as a damage reaction (a common phenomenon) is of little use if the damage is fatal within this time.

The delay in seed production may be due to the very large seed crop which is

produced; after flowering, the acacia may need a rainy season's energy production to mature the crop. The large number of large seeds produced by acacias is apparently associated with the 90 per cent or higher seed destruction by bruchid beetles; it appears that acacias have been singularly unsuccessful in evolving means to reduce this beetle damage. The obligate acacia-ants are of little use in this connection because the ovipositing female bruchids are very persistent. In the newly created but extensive habitat of man's pastures and roadsides, it appears that there is strong selective pressure favoring the shortening of the time for seed maturation; very often the sucker shoots from stumps do not grow long enough for seed production (though they often flower) before they are cut off or burned. If the above hypothesized reason for a year-long seed maturation period is correct, then a reduction in the necessary size of the seed crop, either through increased protection from bruchids or increased seedling survival, should be selected for; the obligate acacia-ants are an obvious instrument through which this selection may take its effect.

(16.) The swollen-thorn acacias are virtually dependent on the obligate acacia-ants for survival in nature. The experimental work with unoccupied swollen-thorn acacias indicates that if the obligate acacia-ants were abruptly exterminated, the acacia population would be drastically reduced to the point of extinction in nearly all locations (e.g., see Tables 2, 3, and 4); the same can be said of the obligate acacia-ants, were the swollen-thorn acacias to be abruptly removed. Other members of the genus *Acacia* do not depend so heavily on other higher organisms; they are not even noted for specific pollinators.

As a by-product of this study, it has become obvious that at the present time natural insect populations can maintain sufficient feeding pressure on a plant population to cause and maintain large morphological and physiological evolu-

TABLE 4. *Mortality of unoccupied stumps (I-1, I-2) and occupied stumps (I-3), between October 18, 1963 and August 6, 1964 (Temascal, Oaxaca, Mexico). Ants removed as in Table 1 (Acacia cornigera × Pseudomyrmex ferruginea, Janzen, 1966a).*

Subplot Date	I-1		I-2		I-3	
	Num- ber alive	Num- ber dead	Num- ber alive	Num- ber dead	Num- ber alive	Num- ber dead
Oct. 18	38	0	31	0	39	0
Mar. 13	22	16	21	10	34	5
Jun. 10	18	20	17	14	28	11
Aug. 6	17	21	13	18	28	11

tionary deviations from the other members of the genus. To a less obvious but significant degree, it can likewise be said that other plants in the community can provide such selective pressure as well. The ant-acacia system happens to be easy to study because the obligate acacia-ants are easily removed; however, there is reason to believe that if one could remove the secondary plant substances and alter the micromorphology of many plants, one would often be able to show a similar immediate dramatic effect of the insects and other plants in the community on the plant species concerned. In a sense, the obligate acacia-ants are the secondary plant substances and micromorphology of the swollen-thorn acacias, and they are the means through which the swollen-thorn acacias interact with a large number of the other organisms in the community. Despite the generally accepted concept that, with the exception of browsing mammals, the physiognomy of plant communities is a direct and total reaction by the plants to physical parts of the environment (fire, water, soil, temperature, wind, etc.), consideration of the ant × acacia interaction system leads to the hypothesis that evolutionary abilities of the entire group of organisms in the community is responsible for the structure and properties of the plants in the community, especially at the microstructure level, operating within the framework of the physical environment.

TABLE 5. *Pseudomyrmex* traits related to the ant-acacia coevolution (worker traits unless otherwise indicated).

A. General features of <i>Pseudomyrmex</i> of importance to the interaction	B. Specialized features of obligate acacia-ants (coevolved traits)
1. Fast and agile runners, not aggressive	1. Very fast and agile runners, aggressive
2. Good vision	2. Same as A 2
3. Independent foragers	3. Same as A 3
4. Smooth sting, barbed sting sheath not inserted	4. Smooth sting, barbed sting sheath often inserted
5. Lick substrate, form buccal pellet	5. Same as A 5
6. Prey items retrieved entire	6. Same as A 6
7. Ignore living vegetation	7. Maul living vegetation contacting the swollen-thorn acacia
8. Workers without morphological castes	8. Same as A 8
9. Arboreal colony	9. Same as A 9
10. Highly mobile colony	10. Same as A 10
11. Larvae resistant to mortality by starvation	11. Same as A 11
12. One queen per colony	12. Sometimes more than one queen per colony
13. Colonies small	13. Colonies large
14. Diurnal activity outside nest	14. 24-hour activity outside nest
15. Few workers per unit plant surface	15. Many workers active on small plant surface area
16. Discontinuous food sources and unpredictable new nest site	16. Continuous food source and predictable new nest sites
17. Founding queens forage far for food	17. Founding queens forage short distances for food
18. Not dependent on another species	18. Dependent on another species group

ACACIA-ANTS

(1, 2, 3, 4, 5, 6.) The entire ant genus *Pseudomyrmex* is characterized by fast and agile worker ants, and the queens are no exception. The evolution of such speed and agility was undoubtedly very important in the movement of the first members of the genus into an exposed arboreal habitat, where visual predators are extremely abundant and a fall means getting lost. The behavior of a single worker *Pseudomyrmex* is much like that of a hunted squirrel, dodging behind objects and to the far side of branches. The ants have large compound eyes that cover one-third to two-thirds of the side of the head, and they often visually locate prey, enemies, and nest markers. Odor trails are rarely used. *Pseudomyrmex* workers forage independently, and bring in entire or fragmented insects, plant nectars, and coccid nectars. They do not solicit the cooperation of other workers in prey capture or retrieval. Two workers contest a

prey object (tug-of-war) until one gets it and then returns to the nest. Foraging workers are constantly picking up small bits of organic matter from the foliage and these are incorporated into a buccal pellet which is fed to the larvae; this is undoubtedly an important food supplement. This ability to collect and consolidate tiny food items from surfaces from which larger items often fall has likely been of importance in the success of *Pseudomyrmex* as an arboreal forager. Usually only the barbless sting is inserted in prey insects; the barbed sting sheath is apparently only rarely inserted. *Pseudomyrmex* workers are well known for their bad sting among people who work with vegetation. Judging from the inordinately large number of apparent Batesian mimics of *Pseudomyrmex*, the sting is well respected by visual predators. The well-developed sting is probably of greater importance as an individual worker defense mechanism than in predation; thus it is

not surprising that it is not barbed. Prey items are generally retrieved entire, and are rarely more than twice the size of the worker. Common items are small lepidopterous larvae, insect eggs, flies, and small beetles, plus unidentifiable insect fragments. While removal of these insects from the tree where the colony is located (in a hollow twig) has some effect, the mere presence of the ants is of equal or greater importance. Phytophagous insects generally display strong avoidance reactions when approached by ants.

The workers of obligate acacia-ants do not differ greatly in the above six characteristics of *Pseudomyrmex*, but they are in addition often extremely aggressive to foreign objects. There are few insects that can outrun or dodge away from an aggressive obligate acacia-ant (Table 6); those few that can do so live in association with the interaction (see Table 1, B-10). Intruders are often located through vision (day) and contact (24 hours). Workers can see small moving insects at distances up to four centimeters, and will even attack shadows from a flashlight at night. Attacking workers often move so fast that they miss their object and are distracted by some other moving worker. When contacted, the object is bitten and stung. This is generally sufficient to cause an insect to leave. However, the excited worker liberates an alarm odor which causes other workers to run much faster and increase their frequency of turning. The net result is a rapid accumulation of workers on the intruder. There is no mutual cooperation among the workers in this attack. Only very small insects are held until dead, and only rarely these are dismembered and some pieces used for food for the larvae; most pieces are dropped off the tree. Mammals are attacked with equal vigor, and the barbed sting sheath is often inserted to hold the ant in place. To humans, the obligate acacia-ants have a much more painful sting than do other *Pseudomyrmex*.

More than 99 per cent of the colony's solid food comes from the Beltian bodies

TABLE 6. Incidence of phytophagous insects on shoots of *Acacia cornigera* occupied and unoccupied by *Pseudomyrmex ferruginea*, between June 13 and July 29, 1964 (Temascal, Oaxaca, Mexico, first part of the rainy season, Janzen, 1966a).

	Occu- pied	Unoc- cupied
Daylight		
No. of shoots examined	1,241	1,109
Percentage of shoots with insects	2.7	38.5
Mean no. of insects per shoot	0.039	0.881
Mean no. of insects per shoot known to feed on <i>A. cornigera</i>	0.036	0.806
Nighttime		
No. of shoots examined	847	793
Percentage of shoots with insects	12.9	58.8
Mean no. of insects per shoot	0.226	2.707
Mean no. of insects per shoot known to feed on <i>A. cornigera</i>	0.220	2.665

that are harvested as single units and taken back to the thorns. Obligate acacia-ants lick the surface of the acacia and make buccal pellets. Not only are all fungal spores, etc., removed, but a sticky material is removed from the newly expanding leaves which allows normal expansion. Necrotic areas on the surface of the plant are chewed off by the workers. Odor trails exist between two different shoots occupied by the same colony and the surface of the acacia very likely has a colony odor; however, it appears that workers use visual orientation on the surface of the acacia as well.

Several points bear consideration in the original evolution of worker aggressiveness. The queens are not aggressive. The prototype acacia that provided the *Pseudomyrmex* colony with a progressively larger and more reliable food and domatia, not only had more workers active on its surface but it had older workers since the members of the colony had to forage less distance from the thorns and subject themselves less frequently to predation and getting lost. Secondly, it is reasonable to expect that there were several

species of *Pseudomyrmex* and other ants living in the thorns of the prototype acacia, and the one that became an obligate acacia-ant was very likely initially either the most aggressive or had the genetic ability to rapidly become aggressive with little selective pressure.

(7.) While attack of plants has not been noted among the *Pseudomyrmex* that are not associated with living plants, obligate acacia-ants habitually bite and/or sting any foreign vegetation that contacts the canopy of the swollen-thorn acacia. Seedling acacias are killed unless they have swollen thorns and nectaries. In addition, the ants kill the vegetation attempting to grow in a circular area below the swollen-thorn acacia (Fig. 1a). This circle is of varying size, depending on colony age, size, and genotype. The net result of this activity is that the swollen-thorn acacia often grows in a cylindrical space that is virtually free of foreign vegetation and the various influences that it can have (shading, mechanical interference, insect pathways, fuel for fires—Janzen, 1966d). Dense stands of swollen-thorn acacias are completely free of other green vegetation.

It is postulated that the reaction to foreign plants is an outgrowth of the aggressiveness to other insects and to strange objects in general. Some nutrients may be obtained from the sap of the chewed plants but since (1) they are attacked even when there is a surplus of nectar and Beltian bodies, (2) all species are attacked, and (3) workers become aggressive to plants after they start attacking insects (aging process), it is unlikely that this is the present-day cause. The selective force for increased aggressiveness against plants is a feedback in exactly the same manner as is selection for aggression towards animals by the obligate acacia-ants.

(8.) The workers of *Pseudomyrmex* display monomorphic allometry (terminology of Wilson, 1953) accompanied by size variation up to about one and a third the length of the smallest worker in the

colony. The size of the workers increases until the first reproductives are produced and then levels off.

The obligate acacia-ants apparently have temporal division of labor. As a worker ages, it moves through a progression of duties in the colony, the last one being patrolling the surface of the swollen-thorn acacia. It is these oldest workers that often are first to encounter foreign organisms. A small but old colony is sometimes more effective in patrolling a swollen-thorn acacia than a large young colony. The presence of workers old enough to be very aggressive may be due to the considerably lower death rate of workers when they are concentrated in the canopy of a swollen-thorn acacia (in contrast to being scattered through the vegetation on foraging activities).

Provided that food is available, the reproductive castes are produced in small numbers on a year-round basis. For the species living in hollow twigs, there is rarely enough food for this. However, obligate acacia-ants generally have enough food throughout the dry season, except at the dry margins of distribution. This continuous production of new queens insures that seedlings and sucker shoots have founding queens in them as soon as a thorn is present on the shoot. More queens mean more ant colonies. The upper limit is apparently set through competition for thorns, and seedling and sucker production by the swollen-thorn acacias.

(9, 10.) The genus *Pseudomyrmex* lives almost entirely in and on living and dead plant structures above the ground. The adaptive radiation into the arboreal habitat is reflected in much of the ants' behavior and morphology (fast, agile, good vision, good sting, buccal pellet formation, slender body, mobile colony, dispersed colony units, etc.). The nest is in hollow twigs and branches with a narrow inside diameter; when vertical, the larvae are either wedged in or hung by dorsal hooked hairs from the walls. The larva has a ventral pouch to hold food particles

while feeding. The colony is often distributed among several hollow branches. When one begins to rot, that portion of the colony is easily moved to some other site previously selected by the workers. They commonly hollow out the pith area of a dead stem. These dead and hollow twigs rarely last over a year without rotting or falling, and thus the colony moves frequently. Except for destruction of the unit containing the queen, destruction of one of the colony portions does not destroy the colony. The thorns of prototype acacias, other plants, and unoccupied swollen-thorn acacias are commonly used by *Pseudomyrmex* that are not associated with living plants. They use these structures like hollow twigs, either cutting their own entrance holes, using natural cracks, or using the exit holes of microlepidoptera or other insects that matured in the thorn parenchyma.

The evolution of nest site preference from hollow twigs to swollen thorns is not a large change for obligate acacia-ants, but extremely important for the interaction. It concentrates the ant colony in the canopy of the acacia, and means that it is most efficient for the ant colony to get its nutrients from the acacia canopy. Even at the lowest level of interaction, the colony is partially protecting the acacia just in its own defense reactions.

The swollen thorn is an excellent domatium (stronger, more predictable in occurrence, waterproof, more permanent, usually bird-proof, etc.) but portions of the colony continue to move as the thorns dehisce. By continually moving into the new green thorns, and gradually phasing out the old thorns, the colony moves upward with the rising acacia canopy. The queen has to move one to three times a year to stay in the biggest new thorn. The mobility of the entire colony is important in areas where the acacias are occasionally cut or scorched, or when the acacia dies of old age. The colony then has to move out of the old colony and into new stump suckers or find a new unoccupied seedling. Very often a large colony is much older

than the shoot that it occupies, and because of its size and age offers maximal protection to the shoot.

(11.) *Pseudomyrmex* larvae can live isolated in glass tubes for two to four weeks without any food or water. This resistance to starvation is important to the species that live in hollow dead branches; the food supply for these ants fluctuates greatly with the seasons. During the dry season, colony size and the number of colony subdivisions is greatly reduced. Even during the rainy season, larvae may have to wait several days between food items.

A strong obligate acacia-ant colony can survive three to five weeks without food and apparently very little cannibalism takes place. The very shrunk larvae readily accept pieces of Beltian body after starving for three weeks. This means that a swollen-thorn acacia can drop its leaves for nearly a month during the dry season without losing its ant colony by starvation. However, the colony may move if another leafy acacia is available. Secondly, the colony can survive in a cut canopy until new suckers are produced by the cut stump. Finally, if some insect happens to eat off all the new growing shoot tips (e.g., *Coxina hadenoides*), the colony can easily starve until more new shoot tips are produced (two to five days).

(12, 13.) The majority of *Pseudomyrmex* species have one egg-laying queen per colony, and the colony contains 100 to 2000 workers when reproductively mature. Determining colony size of the species living in hollow branches is difficult due to its subdivision into several different branches. The queen remains in one branch and the eggs or first-instar larvae are carried to the other parts of the colony. In single-queen colonies, the workers do not tolerate the entrance of new founding queens. This insures that there is a continual production of new colonies, rather than established colonies absorbing the newly produced queens; this avoids large density fluctuations from mortality

of single large colonies, and insures colony dispersal among the vegetation. In view of the difficulty of finding food, when not associated with a living plant, it appears that one queen can easily produce enough larvae to use all the food brought in.

Obligate acacia-ants have single-queen colonies with two to 30 thousand workers in at least four species. Even with abundant food, the colonies do not get much larger. Where conditions highly favor acacia reproduction, the colony may become too dispersed among the many shoots and growth rates are reduced. In at least three species, the colonies will accept new founding queens. This results in a high rate of egg production and a colony with several million workers (several thousand queens) spread over as much as a half acre of pure swollen-thorn acacia vegetation. In areas where the acacias grow well for most of the year, and phytophagous insects are abundant, there is probably strong selective pressure for maximal egg production and acceptance of founding queens by the workers of established colonies. Such a tremendous number of new queens is produced by multiple-queen colonies that there is little danger of the entire queen crop being absorbed by established colonies and abandonment of new seedlings.

(14.) Obligate acacia-ants patrol the surface of the swollen-thorn acacia both day and night. Other *Pseudomyrmex* workers are active outside the nest only during the middle six to 10 hours of the day. Nocturnal activity of obligate acacia-ants is a necessity since much of the damage done to unoccupied shoots is at night. There are distinct rhythms in the density of workers on the surface of the acacia and the peaks coincide with the times of maximum insect activity (dusk and noon) and of nectar flow (dawn).

(15.) Almost no workers are seen on dead branches containing *Pseudomyrmex* nests; on the other hand, obligate acacia-ants are very active on the surface of the

acacia. As many as 25 per cent may normally be outside of the thorns, and up to 50 per cent may leave the thorns under severe disturbance conditions. This difference is directly related to the great dispersion of foraging workers of other *Pseudomyrmex* throughout the vegetation, and the concentration of the activities of the obligate acacia-ants within the acacia canopy; this concentration is possible since all the food and nest sites of the ants are found there. There is a small dispersion of obligate acacia-ants away from the acacia, and it is these ants which find the various unoccupied swollen-thorn acacias that the entire colony later occupies.

It is this concentration of the workers in the acacia canopy, through provision of food (at least nectar) and thorns, which was probably the major step by the acacia in the initiation of the interaction. This, coupled with increased aggressiveness by the ants, is the basic start to an effective ant \times acacia interaction. When the workers are concentrated at one site, they are much less prone to predation since they protect each other by multiple attacks on invaders (lizards, birds, spiders, etc.). Secondly, with a large and predictable food and domatia source at hand, the workers do not subtract grossly from the colony energy economy by "spending their time" patrolling the surface of the acacia.

(16.) The obligate acacia-ants have their food and nest sites dependably provided by the acacia. In view of the fluctuating nature of food density, and extreme competition for food that other *Pseudomyrmex* experience among themselves and with other ants, the obligate acacia-ant colony could not grow large enough to patrol the acacia effectively if it had to depend on its food-gathering abilities off the acacias. Thus the interaction has required a switch to dependency on a plant product—Beltian bodies. The major change is the behavior of harvesting Beltian bodies. In this connection

it should be noted that ants in the genus *Solenopsis* harvest them as well (no connection with the interaction).

The predictable production of many new thorns each year to house the enlarging ant colony is of utmost importance to the system. Unless the obligate acacia-ants nested in the ground, it would be virtually impossible to find enough hollow space near the acacia to house the ant colony.

(17.) Once a founding queen obligate acacia-ant finds an unoccupied acacia, and becomes established in an untenanted thorn, she is assured of a close food source. She has to move only a few centimeters to obtain nectar for herself and to obtain nectar and Beltian bodies for her larvae. Founding queens not associated with living plants forage for food in the vegetation in open competition with other ants. Examinations of bird and lizard intestines, and spider webs, show that there is heavy predation on searching and founding queens. The advantages of having good nest sites and nectar close at hand for founding queens were undoubtedly important in increasing the density of *Pseudomyrmex* colonies on the prototype swollen-thorn acacias.

Severe competition for the thorns on unoccupied acacia seedlings or suckers is common in man-made disturbance sites. The queens interfere with each other when cutting entrance holes and searching the acacia. As many as 100 queens may be found on a single small seedling and these ants spend much time dodging away from each other. Once a queen is inside a thorn, she may still lose it and her brood to any other searching queen which gets into the thorn while she is out collecting food. In areas where many queens are being produced by large mature colonies, seedlings and suckers may go for many months without a new colony being successfully started in them. This may serve as a population regulation mechanism since increased searching queen density lowers both rate of new colony establishment and swollen-thorn acacia seedling

and sucker survival. There is very high mortality of the searching queens on such sites; the system is apparently an artifact of times when swollen-thorn acacias were more widely dispersed (natural disturbance sites) and large numbers of searching queens were necessary.

(18.) The obligate acacia-ants are completely dependent, as a colony in nature, on the swollen-thorn acacias. In the laboratory, glass tubes and honey can substitute for thorns and nectar, but a substitute has not been found for Beltian bodies. The obligate acacia-ants have committed themselves to the fate of the swollen-thorn acacias, provided that something happens to the swollen-thorn acacias so rapidly that the obligate acacia-ants cannot evolve out of the interaction system. However, the obligate acacia-ants are in the rather unique position of being able to evolve characteristics that can clearly affect, in a positive direction, the survival and growth of the swollen-thorn acacia. In a less clear manner, such mutual interference or assistance is probably present in the majority of interspecies interactions; however, it is much less easy to demonstrate since most species leave themselves several alternatives in their interactions with other species. In this connection it is important to note that the obligate acacia-ant is a multipurpose trait of the swollen-thorn acacia (and vice versa) and is involved in its interaction with many other species in the environment. It therefore has a large chance to influence the outcome of these interactions.

A further feedback system is that the presence of an ant colony old enough to produce reproductives indicates that there is a swollen-thorn acacia present that is old enough, or will be old enough, to produce seeds or suckers; that there is a swollen-thorn acacia old enough to produce seeds or suckers is a very strong indication that there is an obligate acacia-ant colony present that is large enough to produce reproductives.

DISCUSSION

The interaction system between obligate acacia-ants and swollen-thorn acacias is clearly an example of mutualism between a higher plant and an animal. The present deductive discussion of the evolution of the traits of the ant and the acacia leads without reasonable doubt to the conclusion that the system evolved through mutually interactive evolution, or coevolution, rather than by chance coincidence in time and space of two highly specialized yet mutually beneficial organisms. A great part of the necessary traits are beneficial to the ants and acacias only when interacting. With the exception of a few other *Pseudomyrmex* that apparently have obligatory interactions with other genera of plants, at least 10 traits of the ant and 14 traits of the acacia are possessed by only those members of the genera *Pseudomyrmex* and *Acacia* that are obligatorily associated with each other. These traits run the gamut from purely morphological (e.g., swollen thorns) to purely behavioral and physiological (e.g., aggressiveness, year-round leaf production); their putative prototypes can be found among other members of the genera *Pseudomyrmex* and *Acacia*, some of which may be presently in the process of coevolving an ant \times acacia interaction system. Neither organism evolved solely to match the properties of the other, but rather there must have been gradual evolution by both the ant and the acacia toward the present-day interaction.

If the coevolution of the ant \times acacia interaction is viewed as a system between two species (or life-forms), rather than a unique case of ant \times acacia coevolution, certain basic properties of interaction systems can be discussed.

1. The coevolution of an ant \times acacia mutualistic interaction is the product of an evolutionary feedback system *par excellence*. There have been a multiplicity of changes in the swollen-thorn acacia which resulted directly in an increase in density or "healthiness" of the occupant

ants and indirectly in selection for the acacia genotype which possessed the changes. There have likewise been changes in the ant which resulted directly in an increase in the reproductive capacity or "healthiness" of the acacia being occupied and indirectly in selection for the *Pseudomyrmex* genotype which exhibited the changes. This system requires two basic components. One of the organisms must supply the other with a requisite (*sensu lato*), and the receiving population must have a mechanism to favor the donating genotype of the donor population. In addition, the requisite is usually a quantitatively defined variable, and the donor can increase its value. For example, the obligate acacia-ant can supply a swollen-thorn acacia's requisite of a means to deter most of the phytophagous insects in the plant community, and can increase this flow from a trickle (taking an occasional insect as prey) to a massive output (keeping the tree virtually free of insects, except for those that can evolve into the system). The ant genotype that does this will be favored by an increased supply of the requisites it receives from the acacia. The swollen-thorn acacia can supply an obligate acacia-ant's requisite of a sugar source, and can increase this flow from a trickle (the tiny output of the tiny nectaries found on many legumes and other plants that lack an obligate relationship with ants) to a massive output. The acacia genotype that does this will be favored by an increased supply of the requisites it receives from the ant.

This system involves selection for a genotype that differs only slightly from the other members of the species' population at any point in the system's evolution. Further, such a system need not involve any long-term changes in total density of either population, although it does appear that the ant \times acacia coevolution has increased both the density and ranges of the species involved in man-made disturbance sites. The cumulative result of this selective system is a set of populations which are greatly affected if

a trait necessary to the interaction is suddenly removed (e.g., remove the ant's aggressiveness or the acacia's Beltian bodies).

The system is self-reinforcing, operating through the medium of the other member of the species pair. Systems of this type are very common in nature, though they usually involve one-way, rather than two-way, energy flow. The evolution of the traits of predator and prey is such a case. Here, success in either of their interactive operations (prey capture by predator, or prey escape by prey) favors the genotype that was successful, causing selection against the unsuccessful genotype in both populations. This in turn promotes selection for an improvement of the successful genotype. For example, if a predator catches a prey organism, it usually promotes the prey genotype that was not captured. However, this latter prey genotype is presumably harder to capture, and the predator must then evolve further capturing abilities. Such a system is balanced by the evolution of the prey in the same manner, changing hosts or predators, inefficiency, etc. In a mutualistic system such as the ant \times acacia interaction, both organisms are simultaneously successful and thus both genotypes responsible for the success are favored. It should be noted that both members of the mutualistic pair have predator-prey (*sensu lato*) evolutionary systems with other organisms outside of the ant \times acacia interaction system.

2. The ant \times acacia system contains an excellent example of convergence or parallelism, and if the entire Pseudomyrmecinae and other ant-plants are considered, the case is even stronger. Based on morphological similarity, the obligate acacia-ants are composed of two groups. *Pseudomyrmex nigropilosa* is the only member of one group, and appears to be a species which is "evolving into" the ant \times acacia interaction system. It is morphologically very similar to a large group of *Pseudomyrmex* that are not associated with living plants. Since it offers no protection

to the swollen-thorn acacia that it occupies it must be regarded as parasitic on the other obligate acacia-ant species which keep the swollen-thorn acacia population alive. The other obligate acacia-ants are so similar morphologically and behaviorally that they are very likely evolved from a common ancestor which was an obligate acacia-ant. There is no reason to believe that the conditions of living in association with a swollen-thorn acacia are so exacting that one would expect the *Pseudomyrmex* becoming involved in the interaction to converge as strongly in their morphology as are these obligate acacia-ants (see Janzen, 1966c).

The swollen-thorn acacias, if flower and fruit diversity are to be trusted as indicators of lineages, represent at least five independent evolutions into the system: *Acacia cornigera* and *Acacia sphaerocephala*; *Acacia hindsii* and *Acacia collinsii*; *Acacia melanoceras*; and two undescribed species.

A progression for the production of these interactive species is hypothesized as follows. The coevolution of an obligate interaction between one species of *Pseudomyrmex* and one species of *Acacia* occurred somewhere in the New World tropics. The simplest further complication lies in what apparently occurred to produce *A. cornigera* and *A. sphaerocephala*, two extremely similar species occupied by *Pseudomyrmex ferruginea* in eastern lowland Mexico. *A. cornigera* is a species of wetter areas and *A. sphaerocephala* a species of drier areas. At some time in the past, they apparently represented two populations of an ancestral species (or perhaps *A. cornigera* or *A. sphaerocephala*) which became genetically isolated and at present are just beginning to reinvade each other's ranges with very little introgression. A similar situation appears to have occurred with *A. collinsii* and *A. hindsii*. Once this occurred, other acacia lineages must have entered the system. Once the interaction system is present at the same locality as another acacia with the preadaptations to become involved,

such involvement is facilitated by three means. (1) The obligate acacia-ant will readily occupy another acacia which develops swollen thorns, nectaries, and Beltian bodies in sufficient numbers to support the ant colony. If such resources are insufficient in quantity on one plant but there is a nearby swollen-thorn acacia, the colony will live in both species of plant at the same time. (2) The swollen-thorn acacias frequently form interspecific hybrids with other acacias; the traits for enlarged nectaries, swollen thorns, and Beltian bodies are readily transferred through introgression and the hybrids apparently produce viable seed (Janzen, 1966b). (3) The trait of extreme susceptibility to insect attack is also transmitted and this makes it imperative that the hybrids, to survive, be thoroughly occupied. The entire system described above appears to be occurring at the present time between *A. cornigera* and *A. chiapensis* in southwestern Veracruz, Mexico.

To become thoroughly occupied, the acacia species must reinforce the possession of nectaries, swollen thorns, and Beltian bodies by evolution on its own, or by very thorough incorporation of the donated traits into its own genotype. The population of acacias which has newly received the swollen-thorn acacia traits will likely have a different total distribution from the donor swollen-thorn acacia; thus, the obligate acacia-ant, in following the incorporation of traits into its new host plant's population, will undoubtedly find itself under new environmental conditions. If it can tolerate these, and the acacia can maintain the swollen-thorn acacia traits over at least part of its range, the acacia will likely find itself being a swollen-thorn acacia, in spite of itself, so to speak. It should be noted that this will, in all likelihood, result in such by-product effects as changing the acacia's range to those areas where the interaction can survive, and extinction or speciation of the portions of the population living in areas where the interaction cannot occur. Under such circumstances, there is a chance that

the obligate acacia-ant species will be cut off from its parent population, leading to further speciation among the ants.

3. There is a growing body of literature which strongly suggests that the chemical and microphysical properties of the vegetative parts of plants may be evolved in partial or entire response to the use of the plants as energy sources and substrates by insects (see Southwood, 1961; Beck, 1965; Stark, 1965; and Ehrlich and Raven, 1965; and included references). It appears that the swollen-thorn acacias have substituted the abilities of the obligate acacia-ants for many of the physical and chemical traits that other acacias use in their defense; this is strong evidence that these properties exist. In fact, the swollen-thorn acacia gains properties from the ants that other members of the genus *Acacia* do not possess. The demonstration of these two statements was made possible in a clear manner only through the ease with which the obligate acacia-ants could be removed from the acacia. To perform similar experimental demonstrations of the significance of apparently meaningless chemical and physical properties of plants will require removal of the secondary plant substances or alteration of the micromorphology without directly damaging the plant. This is exceedingly difficult, and becomes even more so if one tries to remove as many factors as the obligate acacia-ant provides.

The ant \times acacia system is representative of plant \times insect interactions in that the swollen-thorn acacia has a small group of insects which feed on it in spite of its normally deterrent properties (obligate acacia-ants). These insects do not do enough damage to remove the acacia from the habitat although they take enough of the acacia to keep their own populations in existence. The actual numerical values of such a set of mutually sensitive energy flows are primarily a function of their position in evolutionary time, the evolutionary abilities of the organisms in the community, and their energy requirements at any given time of year. The energy

flow values change as the plants and insects evolve in and out of interactions. Further, when the ants are removed, not all the insects in the community feed on the unoccupied swollen-thorn acacia; such attack is generally only by those that feed on closely related plant species or genera, or those that normally show long and broad host plant preference lists. It is the net effect of all of these insects coming from other host plants to feed on the unoccupied swollen-thorn acacia that mounts sufficient continuous feeding pressure to kill the acacia. Or, stated in another way, the behavior of the ants places the occupied swollen-thorn acacia low on the host lists of all but a very few insects; when the ants are removed, this suddenly moves the swollen-thorn acacia very near the top of the host preference lists of many insects that normally feed on closely related plants, or have broad food tolerances. The insects that feed in the presence of the ants are rarely found on unoccupied swollen-thorn acacias; such plants have generally been so badly damaged that the intact foliage preferred by these insects is absent.

In addition to affecting the use of the swollen-thorn acacia by insects, the obligate acacia-ants also affect its interactions with other plants, especially vines. Other plants in the lush second-growth community keep their canopies sufficiently free of vines by various structural and behavioral traits. These traits are singularly difficult to recognize and demonstrate. They apparently include such things as drooping leaves with very smooth upper surfaces, off which vine tendrils easily slide while the supple and smooth woody stems move in the breeze. This results in the general vine layer being slightly below the rapidly rising canopy rather than over it. However, at times the vine mat actually does cover and heavily shade the woody vegetation. The swollen-thorn acacias serve as excellent vine supports when unoccupied. Their stiff lateral branches adorned with thorns and compound leaves make excellent attachment points for

vines and are quickly covered and bound into the vine mat. On the occupied swollen-thorn acacia, the vine leaders and tendrils are killed by the obligate acacia-ants when they come in contact with the acacia. The effect can be very dramatic when the swollen-thorn acacia grows up through a solid vine mat that is shading all the neighboring plants. The pruning of lateral branch tips from neighboring shrubs, when they contact the swollen-thorn acacia, is another function of the obligate acacia-ants which aids the acacia in its competition with other plants (reduces shading).

A by-product of the pruning activities of the obligate acacia-ants is the deterrent effect of the clear area around the acacia on certain types of fires (Janzen, 1966d).

4. The ant \times acacia interaction system is possible because of various preadaptations. Both ant and acacia display many morphological and behavioral traits which are necessary to the interaction as it now exists and which apparently were possessed before the species became more interrelated than are the many other species of *Pseudomyrmex* and *Acacia* at present. Further, nearly all of the traits of the ant and the acacia which are important to the interaction can be seen to be the results of gradual reduction or magnification of some pre-interaction property. The three clear exceptions are the Beltian bodies, their use by the obligate acacia-ants, and the attack on foreign plants by the ants.

That the Pseudomyrmecinae are exceptionally well preadapted to the evolution of such ant \times plant interactions is suggested by the existence of at least five apparently independently evolved pseudomyrmecine \times plant mutualistic interactions (*Pseudomyrmex* \times *Acacia*, *Pseudomyrmex* \times *Triplaris*, *Pseudomyrmex* \times *Tachigalia*, *Pachysima* \times *Barteria*, and *Viteticola* \times *Vitex*) and only a few doubtful cases in all the other ant subfamilies. It must be stressed that only the first of the five has been experimentally demonstrated, but the

descriptions in the literature on the others hint strongly that they too are mutualistic. There remain a large number of ants in the Pseudomyrmecinae and other subfamilies that receive some of their requisites directly from plants, and though less obvious, it appears that there may be many plants besides the classic ant-plants which receive some protection from ants and other predaceous Hymenoptera (Janzen, 1966e).

It appears that in most wet tropical lowland communities there is ample "room" for the presence of more ant \times plant interactions. In view of the many cases where it is extremely difficult to demonstrate clear mutualism, it appears that the active evolution of such interactions is now taking place. An ant species which enters into such an interaction generally removes itself from the apparently highly competitive interactions with other foraging ants and other insects, and places itself in a generally more isolated and more immediately reliable fraction of the habitat. It may at the same time make room for expansion of existing generalized ants or the entry of a new species. By this method species density of the ant community may increase. However, species density of the insects that feed on the newly occupied plant will have to decrease, or else they will have to shift their population structures. Thus it is that one cannot predict increases or decreases in total species density through the evolution of ant \times plant interactions, but in general the complexity of the community increases and this may be associated with an increase in species density.

5. As can be seen from the concluding paragraph of the last section, a study of this type has a bearing on the problems of high species density in the tropics. It was earlier noted that as one approaches areas with a progressively longer dry season, the ant \times acacia system (and thus its members) drops out because the acacia cannot hold its leaves long enough to keep the ant colony alive, and the unoccupied shoot does not survive to maturity due to

insect damage. Though less thoroughly studied, the same system appears to be operating as one moves from warm to cool areas (altitudinal or latitudinal); in this case, the ant is not sufficiently active in cool weather to deter the more cool weather adapted phytophagous insects and vertebrate browsers, and thus the acacia receives more damage than it can tolerate and the ant colony starves to death due to lack of leaf products (slower acacia growth as well in cool weather).

As one moves gradually out of warm and moist areas, the complexity and number of plant-insect interspecies interactions appears to decrease per unit area; this is apparently most strongly associated with the gradual reduction in standing biomass produced over the year. As the fluctuations in the physical environment increase and their predictability decreases, and as the standing biomass decreases, the conditions for the evolution of both numbers and quality of interspecies interactions decreases. This is apparently in part due to failure of species because they cannot evolve further to tolerate the physical aspects of the environment. There is, however, another and less obvious reason: the more genetic environment (organisms) there is to evolve with and to match, the more precise can be the evolved interaction, and the more efficiently the given quantity of biomass can be partitioned among the various species concerned. In such a system, the more uniform and predictable the physical environment, the more precise can be the interaction among species. While so much more diverse than the physical environment, the biotic environment (total genetic background) is nevertheless much more predictable in many respects and thus the more biotic environment present, the more complex interactions that can be evolved; this is of course circular in the sense that the more complex biotic environment fosters a more predictable one, and vice versa. Upper limits to such complexity are set by such things as the size of the organisms,

the energy requirements of their minimum-sized populations, their own predictability, etc.

Thus, as one goes from the "tropics" to areas with proportionately less and less biotic environment, and more severe unpredictable physical environments, the members of the ant \times acacia interaction system gradually disappear. In certain areas there are as many as four species of obligate acacia-ants and three swollen-thorn acacias at the same site (Janzen, 1966b, 1966c). It is characteristic of these distributions that as one moves toward the margins of distribution of swollen-thorn acacias and obligate acacia-ants, all the species but one ant and acacia eventually drop out, and finally these last ones disappear. The point at hand appears to be that the non-uniformity and fluctuations in the physical environment take their toll of species as one moves out of the wet and warm tropics by the breakdown of interaction systems as well as by being inimical to the individual species' requirements.

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