ABSTRACT

BENJAMIN ELIJAH CARTER
Ant-Plant Interactions: Mutualism or Uneasy Balance of Exploitation?
(Under the Direction of DR. C. RONALD CARROLL)

The interaction between myrmecophytes and their obligate ant colonies, particularly that between ants and acacias, has been a popular example of a mutualism for many years. However, emerging evidence suggests that this interaction is not as simple as was once thought. Myrmecophytes of both the New and Old World are examined with respect to those organisms that are associated with the ant-plant interaction in order to explore the full range of the nature of the interaction. The two extremes of pure mutualism and outright parasitism can both be observed, in addition to varying steps in between. Notably, the plants have never been observed to take advantage of the mutualism in a parasitic manner, but they have been shown to have the ability to maintain mutualism through the use of exclusion filters. Quantitative experiments are cited to support these findings where available, and suggestions are made as to what further research could be done to provide further insight into the nature of myrmecophyte interactions.

INDEX WORDS: Insect-plant interactions, Mutualisms, Parasitism of mutualisms, Myrmecophyte, Ant-plants, Plant-ants, Acacia, Pseudomyrmex

ANT-PLANT INTERACTIONS: MUTUALISM OR UNEASY BALANCE OF EXPLOITATION?

by

BENJAMIN ELIJAH CARTER

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BENJAMIN ELIJAH CARTER

Approved:

Dr. C. Ronald Carroll December 12, 2008
Dr. C. Ronald Carroll Date
Faculty Research Mentor

Approved:

Dr. Mark Bradford December 12, 2008
Dr. Mark Bradford Date
Reader

Approved:

Dr. David S. Williams December 17, 2008
Dr. David S. Williams Date
Director, Honors Program, Foundation Fellows and
Center for Undergraduate Research Opportunities

Approved:

Dr. Pamela B. Kleiber December 17, 2008
Dr. Pamela B. Kleiber Date
Associate Director, Honors Program and
Center for Undergraduate Research Opportunities

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INTRODUCTION

The scientific community has long used the interaction between swollen-thorn acacias, and their resident ant colonies as a prime example of mutualism (Janzen, 1966a). Indeed, the ant-acacia interaction is very specific, and evidence suggests all manner of benefits for both organisms including food and shelter for the ants (Janzen, 1966a; T. P. C. H. S. Young, Lynne A. Isbell, 1996) as well as defense from herbivory (Brown, 1960; Janzen, 1966a; Stapley, 1998), encroachment by vines (Janzen, 1966a), and fire (Janzen, 1966b) for the acacia. In recent years, many such textbook examples of mutualism have, under closer scrutiny, proven not to be true mutualisms at all. Studies of both New and Old world myrmecophytes and their obligate ant colonies provide evidence that some species of ant are more beneficial to the ant-plants than others and that, in fact, some ants are quite harmful. Those ant species that inhabit acacias, but do not provide as great a benefit for the plants as other (competing) ant species are not mutualists at all; they act as parasites of the mutualism.

Background:

Acacias have compound leaves and many have stipular spines, which in the case of some neotropical species including *Acacia cornigera*, *A. collinsii, A. hindsii,* etc., and at least one African species, *Acacia drepanolobium,* become enlarged in some parts of the plant. Various ant species are able to make entrance holes in these enlarged thorns, which then become domatia for large numbers of ants (Brown, 1960; Janzen, 1966a; T. P. C. H. S. Young, Lynne A. Isbell, 1996).

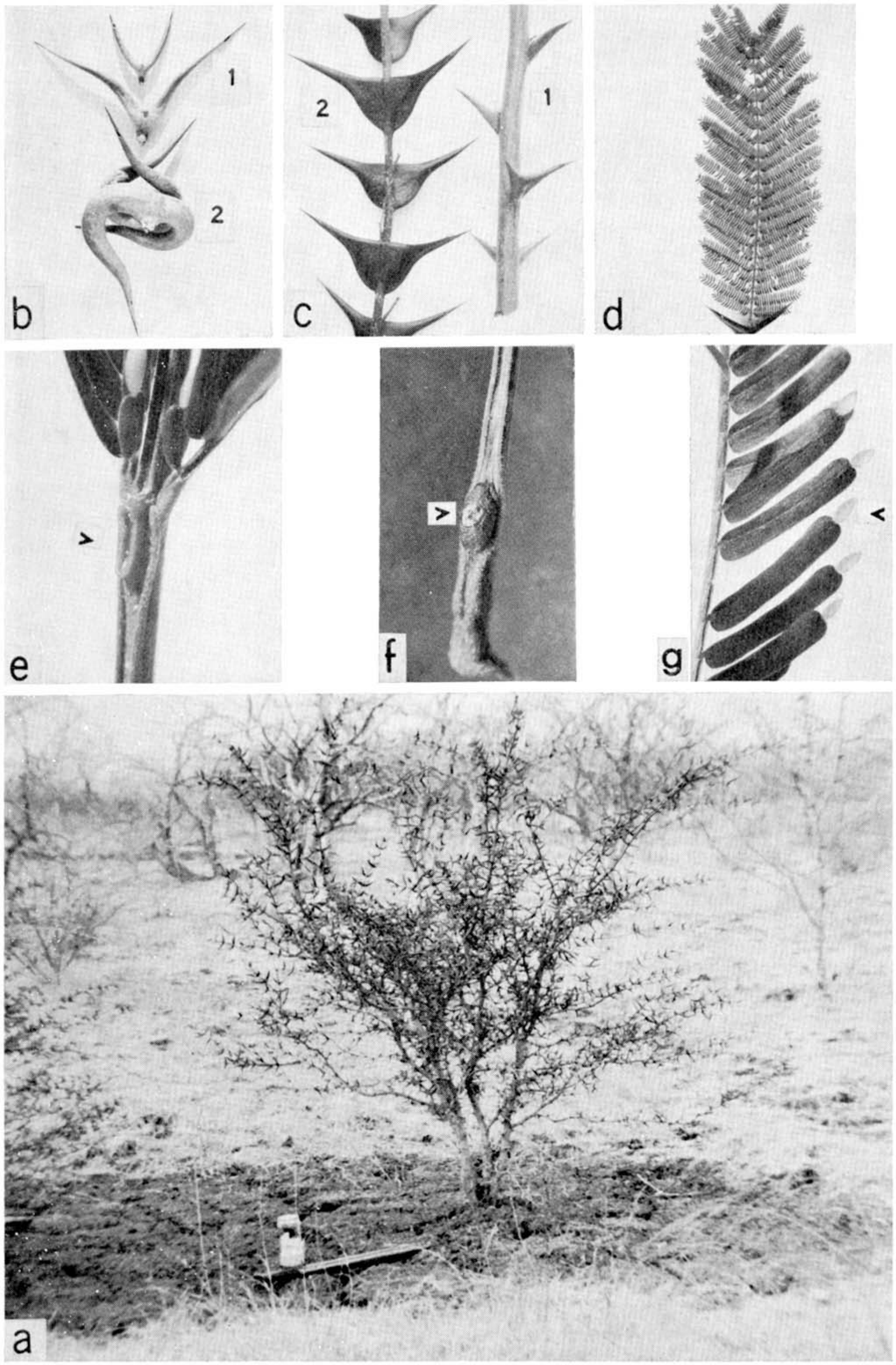

Fig. 1. a. *Acacia collinsii* in a heavily grazed pasture in southwestern Nicaragua. Note bare basal circle cleared of vegetation by *Pseudomyrmex nigrocincta*. b. *Acacia cornigera* type A (1) and type B (2) thorns; same tree, Veracruz, Mexico. c. *Acacia hindsii* type Z (1) and type B (2) thorns; same 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 pinnules of *Acacia cornigera*, same seedling as f.

(Janzen, 1966a)

Acacia trees in both the New and Old World tropics have extrafloral nectaries, which provide sugar for the ants (or any organism that feeds from them). New World acacia-ants also harvest food in the form of protein- and lipid-rich expanded tips of leaflets (Beltian bodies), which can be utilized by ants so that they do not have to leave the acacia to acquire these dietary necessities (Janzen, 1966a). However, Beltian bodies are not produced by *A. drepanolobium*, the African whistling-thorn acacia. The ants inhabiting this acacia must forage outside the acacia for insects and the like.

In the Neotropics specifically, acacias are more common in pasture and early second-growth forest communities. The swollen-thorn acacias typically produce leaves almost year-round, thus keeping the ant colony in constant supply of food, and these acacias in particular seem to lack the characteristic bitter taste of other acacias. This observation leads to the possibility that the swollen-thorn acacias may lack some “secondary” defensive substance. It has been postulated that such a loss of expensive compounds may be due to plant defense being adequately handled by the swollen-thorn acacia’s obligate ant colony (Janzen, 1966a).

It has been proposed that the formation of stipular spines as well as the development of an association with ants are defensive measures by the acacias against the threat of browsing mammals (Brown, 1960). This hypothesis is supported in a number of ways. First, there is a distinct lack of characteristic spines or obligate ant colonies in the acacia species of Australia, which lacks the browsers of the Neotropics and Africa (Brown, 1960). Second, quantitative experiments regarding browsing efficiency of mammals in the presence of thorns, ants, and both, support the conclusion that both these traits reduce the effectiveness of browsing by large mammals (Stapley, 1998). However, the presence of thorns creates an ideal “trellis” for vines which could cover the small acacia trees. Acacia ants aggressively “prune” vine tips that touch the acacia thus preventing vine encroachment. This behavior may be the fundamental basis for some acacia ant species removing vegetation under the acacia indirectly creating a kind of firebreak.

Both Neotropical and African acacias also face other problems: herbivory by insects, and shading out by neighboring vegetation. Ants have been observed to prevent most insects from damaging the leaves, and those insects that manage to persist through the presence of the ants are likely specially adapted to take advantage of the situation (Janzen, 1966a). In addition, the resident ants will maim any foreign vegetation that touches an ant-occupied acacia. The ants will even remove all vegetation from a circle around the base of the acacia (Janzen, 1966a). This process not only destroys potential nutrient and light competitive plants, but also helps to minimize damage to the acacia from small brush fires (Janzen, 1966b).

It is also worth noting that in addition to the few insects that still feed on acacias, a number of other animals spend time in acacias. The social wasp, *Perachartergus aztecus*, nests in acacia trees (Espelie, 1988). Several species of birds frequent acacias as well (Janzen, 1969; B. E. Young, Michael Kaspari, Thomas E. Martin, 1990). Some of these birds prey on acacia-ants, while others aid in seed dispersal for the acacia (Janzen, 1969). Some research suggests that birds may even have a role in pollination of acacia trees (Knox, 1985). The birds and wasps gain access to acacias as nest sites by exploiting that ants' trait of accommodating to repeated small disturbances. The acacia trees are found primarily in environments that have strong trade winds that during the dry season are continually moving the acacia branches and foliage. If the ants rushed to defend the tree every time the wind moved a leaf or branch the ants would soon exhaust their energy supply. Therefore, it is not surprising that the ants quickly stop responded to repeated small disturbances. Birds will often initiate nest construction in the acacia by making a series of short visits and once the ants stop responding the bird settles down and begins nest construction in earnest. In this way, the birds gain access to the acacia and benefit from the aggressive response of ants to potential predators such as snakes.

Developments:

The conventional view holds that the interaction between myrmecophytes and their obligate ant colonies is a prime example of a coevolved plant-animal mutualism. However, more and more evidence is surfacing that reveals that the interaction is simply not so straightforward. Species-wide differences in behavior or demeanor can affect how an ant behaves as an inhabitant of an ant-acacia. Increased aggressiveness, for example, might make a particular species of ant better at defending an acacia. Such differences might make certain ant species better mutualists than others (Frederickson, 2005). Of a group of possible inhabitant species, all species but the best may create opportunity cost for the acacia by preventing access to the best mutualist. According to this way of thinking, all species but the best mutualist could be regarded as parasites of the mutualism (Yu, 2001).

There are two possible processes for interaction in ant-plants: mutualism, or some level of parasitism of the mutualism. Exploration and discussion of ongoing research in both New and Old World acacias and a few similar myrmecophytes will reveal the true nature of interactions between ants and myrmecophytes, and if any one species tends to benefit more than another.

DISCUSSION

Several species of ant inhabit the New World acacias, including *Pseudomyrmex ferruginea*, and *Pseudomyrmex nigropilosa*. Other ants of the genus *Pseudomyrmex* also enjoy the benefits of interaction with ant-acacias (Janzen, 1966a, 1975). Several different ant species inhabit the Old World acacias as well, including *Crematogaster mimosae*, *C. sjostedti*, and *C. nigriceps* (M. L. Stanton, T.M. Palmer, T.P. Young, 2002; T. Y. a. M. Stanton, 1999; T. P. C. H. S. Young, Lynne A. Isbell, 1996). While the specific cases discussed in the introduction are considered to be “purely” mutualistic, there are many documented cases of ant-plant parasitism, as well as of other organisms taking advantage of, and perhaps parasitizing, the aforementioned mutualism.

These organisms, existing outside the ant-plant interaction, include the wasp, *P. aztecus*. The presence of wasps can be construed as a further benefit for the acacia, since browsing mammals would be even less likely to browse from a plant with a wasp nest and a resident ant colony than they would be to browse from a plant with an ant colony alone. The wasps likely do very little to hinder the ants. If anything their nests might provide a very slight obstacle for ants as they patrol the plant. Possible benefits for the wasps nesting in the acacia are unclear, but at the very least the relationship is one of commensalism between the acacia and the wasp. Chemical analysis of the cuticles of the wasps and ants, as well as the surface of the wasps’ nests and acacia thorns, reveal that similar hydrocarbon compounds are present in all four. This similarity suggests that the ants may tolerate the presence of the wasps through evolved chemical trickery on the part of the wasp (Espelie, 1988). However, there is a lack of behavioral studies to back up this assertion, and so there is no evidence outside of the chemical similarity to verify the claim. This relationship, then, may not be a case of pure mutualism, but rather appears to be more a case of asymmetric or incomplete mutualism, or perhaps even commensalism.

The bird association is slightly less clear. Birds take advantage of ant-plant mutualism (in the Neotropics, at least) by consuming the ants, which would not be present if they were not involved in the mutualism. However, the birds also benefit the acacia by distributing acacia seeds (Janzen, 1969). Some research even suggests that birds play a role in pollination of acacias, and it has been proposed that extrafloral nectaries may have evolved in order to aid in this process (Knox, 1985). In addition, some birds take advantage of the ant-acacia relationship by nesting in specific acacia trees. The birds' nests represent, like the wasp nests, little more than a minor inconvenience for the obligate ant colony, while the birds gain the same protection that the ants afford the acacia (B. E. Young, Michael Kaspari, Thomas E. Martin, 1990). The acacia is not greatly affected in this particular relationship, and so this situation, too, can be thought of as a case of commensalism, although predation of the ants is a form of parasitism, and seed distribution and pollination are forms of mutualism.

Another interesting study involves a highly adapted myrmecophyte and a beetle acting as parasite of its ant mutualism. The *Piper* ant-plants of tropical forests provide protein and lipid-rich bodies and shelter for *Pheidole bicornis* ants. However, the plants have developed the unique characteristic that they only produce the protein-lipid bodies when inhabited by their obligate ant. This may be an adaptation to avoid wasting resources before colonization, or even a specific adaptation to avoid parasitism of its mutualistic relationship with *P. bicornis*. The beetle species of genus *Phyllobaenus,* though, have developed the ability to "fool" the plant by stimulating the production of protein lipid bodies, which they then use themselves. The beetles also consume the ant brood, and take advantage of nesting areas on the plant (Letourneau, 1990).

These behaviors by the beetle affect both ant and plant. This resourceful beetle has developed the ability to parasitize both sides of the ant-plant mutualism.

Of course, the main focus of this paper is not to explore the relations of other organisms to ant-plant mutualisms, but if organisms coming from outside the interaction are so able to take advantage of one or both sides of the symbiosis, it might be just as easy for one partner to take advantage of the other. Research in Central America has revealed that different species of ants do, in fact, behave differently towards acacias. *Pseudomyrmex nigropilosa* behaves in a manner very similar to that of ants that do not associate with living plants, yet it will inhabit acacias, taking advantage of domatia, extrafloral nectaries, and even Beltian bodies (Janzen, 1966a). *P. nigropilosa* do not, however, defend the acacia from foreign vegetation and herbivores as the acacia's typical obligate ants would (Janzen, 1975). The obligate ants would provide the maximum benefit to the host plant, and any species that provides reduced benefits, yet still associates with the host plant, must be regarded as a parasite of the mutualism (Yu, 2001).

Another study in the tropics regards a less common acacia species, *Acacia mayana*. Its typical plant-ant is, as in the previous case, usually *P. ferrugineus*. However, the generalist ant *Camponotus planatus* will also inhabit the swollen thorns of *A. mayana*, but does not provide protection from herbivory, making it a parasite rather than a mutualist. Not only is *C. planatus* a parasite, it is a highly effective one, displacing *P. ferrugineus* over 99% of the times that they come into contact. *Camponotus planatus* also collects nectar from extrafloral nectaries, but does not harvest Beltian bodies. It has been advocated that the requirement of larval adaptation in order to properly utilize the Beltian bodies might suggest that Beltian bodies are somewhat resistant to exploitation by generalist ants (Raine, 2004). However, it has been documented that some ants that are not of the genus *Pseudomyrmex* do, in fact, harvest and use Beltian bodies, specifically the genus *Solenopsis* (Janzen, 1966a). The harvesting of Beltian bodies by these ants is not well documented, however, and so it is difficult to describe the nature of the relationship between *Solenopsis* ants and Neotropical acacias.

A similar situation, though more complex than the above, has been observed in the African Whistling-thorn acacia, *A. drepanolobium*. This acacia is inhabited, apparently successionally, by three different ant species of the genus *Crematogaster*: *C. mimosae, C. sjostedti,* and *C. nigriceps* (T. Y. a. M. Stanton, 1999; T. P. C. H. S. Young, Lynne A. Isbell, 1996). There is interesting competition among these species with regard to the colonization process, and trade-offs are apparent. Founding queens of *C. sjostedi*, the competitively dominant species, rarely attempt to establish independent colonies. Queens of *C. mimosae*, the second-most-dominant species, form colonies in a disproportionate number of small, low-quality saplings, while the least competitive species, *C. nigriceps*, colonizes a large number of empty mature acacias (M. L. Stanton, T.M. Palmer, T.P. Young, 2002).

The behavior of these species once established is even more fascinating. *Crematogaster nigriceps* actively destroys axillary extrafloral nectaries and flowering structures in addition to any foreign herbivores. The forced redistribution of resources that would normally be used for reproduction leads to increased production of terminal shoots (and enlarged thorns), and healthier leaves, but also leaves *A. drepanolobium* effectively sterile (T. Y. a. M. Stanton, 1999; T. P. C. H. S. Young, Lynne A. Isbell, 1996). This pruning behavior may indeed be an adaptation to avoid potential contact with neighboring trees containing competing ant species, since *C. nigriceps* is a poor competitor (T. P. C. H. S. Young, Lynne A. Isbell, 1996). The pruning also increases the production of new extrafloral nectaries, of which *C. nigriceps* reap the benefits. Thus, this species has become a parasitic one, harming the acacia by limiting its reproductive ability while enjoying greater nutritive rewards than if the ants simply defended against encroachment (T. Y. a. M. Stanton, 1999).

C. sjostedti, the strongest competitor in terms of colonization, is the poorest candidate for a defender of the host plant. These ants do effectively nothing to prevent herbivory of *A. drepanolobium*. It is interesting to note that unlike the other species which nest in this particular acacia, *C. sjostedti* does not nest in the swollen thorns, but rather in the hollow spaces of dead or damaged limbs. Thus, when parts of the acacia die, for example, because of uncontested herbivory, *C. sjostedti* is provided with more living space (T. Y. a. M. Stanton, 1999). Thus, *C. sjostedti*, taking advantage of the mutualism by outcompeting the other ants, has become a parasite of the mutualism just as *C. nigriceps* is. This feat is accomplished by exploiting the acacia to gain more living space while doing nearly nothing in return.

Crematogaster sjostedti and *C. mimosae* both tend adult scale insects which feed off of the acacia. The ants, in turn, feed off of the honeydew secretions from the insects. Tending of insects such as these is inconsistent with the typical view of co-evolution of mutualisms (T. P. C. H. S. Young, Lynne A. Isbell, 1996). An interesting side note: it has been proposed that extrafloral nectaries evolved in response to the tending of scale insects and that they function in order to provide an alternative sugar source so that the ants need not tend scale insects (Becerra, 1989). However, given the data regarding these parasitic ants, this hypothesis seems somewhat unlikely. Parasitism and the consumption of whole nectaries (not just the nectar) by the another common plant-ant, *Tetraponera penzigi* (T. P. C. H. S. Young, Lynne A. Isbell, 1996), leads to the conclusion that nearly all of the ant species associated with *A. drepanolobium* are parasitic in nature! Perhaps the swollen thorns are a remnant from a time when the mutualism was more balanced, or perhaps some necessary aspect of the “mutualism” remains intact enough for the thorns to still be important.

Table 1:

The table below shows different ant taxa, the way each one interacts with its myrmecophyte host, and a statement regarding the nature of their relationship overall. Species are classified as mutualists if they provide benefits but do no harm to the acacia. Species are classified as parasitic on the mutualism if they provide benefits, but displace species that would be more beneficial for the acacia. The species regarded as very parasitic harm the acacia while providing little benefit. The nature of the genus *Solonopsis* is unknown because there are not enough data to draw conclusions regarding the nature of this genus' relationship to myrmecophytes. Note that while *Crematogaster mimosae* tends scale insects, which is likely less than ideal for the acacia, it is also the species that provides the greatest benefit to the acacia, and thus is not regarded as a parasite of the mutualism.

New World

Ant Taxa	**Behavior**	**Nature of Relationship**
Pseudomyrmex ferruginea *P. nigrocincta*	Inhabits domatia, uses extrafloral nectaries, uses Beltian bodies, defends against herbivores and encroaching vegetation	Mutualistic
P. nigropilosa	Inhabits domatia, uses extrafloral nectaries, uses Beltian bodies, provides no defense	Very parasitic on the mutualism
Camponotus planatus	Inhabits domatia, uses extrafloral nectaries, provides no defense, displaces *P. ferruginea* 99% of the time.	Parasitic on the mutualism
Solonopsis (various)	Harvests Beltian bodies	Unknown

Old World

Ant Taxa	**Behavior**	**Nature of Relationship**
Crematogaster mimosae	Defends tree against herbivory, tends scale insects	Mutualistic
C. nigriceps	Defends tree against herbivory, destroys flowering structures.	Parasitic on the mutualism
C. sjostedti	Outcompetes other ant species, does not defend against herbivory, nests in hollow or dead branches, tends scale insects	Very parasitic on the mutualism
Tetraponera penzigi	Consumes whole nectaries	Parasitic on the mutualism

One difference of note between the Old and New World acacias is that Old World acacias like *A. drepanolobium* lack any protein-lipid bodies to supplement the ants' diet (T. Y. a. M. Stanton, 1999). The question is: why not? With no Beltian bodies present, ants must forage for protein and often harvest other insects. It has been speculated that the discarded insect parts from the ants' foraging efforts might serve to fertilize the acacia, but no experiments have been conducted to confirm or refute this assertion (T. Y. a. M. Stanton, 1999). Perhaps *A. drepanolobium* is simply conserving valuable resources rather than expending them on species that are parasitic anyway. This raises an interesting question: we are well aware that ant species are able to adapt to take advantage of the ant-plant mutualism, but can plants adapt to maximize their benefits?

A quantitative study of several (myrmecophytic) taxa of *Leonardoxa* in the tropics of Cameroon reveals that these taxa have developed exclusion filters that can effectively stop colonization by ants that are not of a plant's preferred species. In *Leonardoxa*, a structure called the prostoma forms a handy entranceway for ants to excavate a place to enter the domatia. The prostomas of different taxa, however, are of different dimensions. Precise measurements of prostoma dimensions can be compared to corresponding measurements of different ant species. The findings reveal that the plant and ant species fit together like a lock and key (Brouat, 2001). Though this specific example does not apply to *Acacia* taxa, it suggests the possibility that a similar, though perhaps less obvious, process can take place in acacias.

CONCLUSIONS

Ant-plant interactions, in particular the interaction between ants and acacias, have long been touted as prime examples of mutualisms (Janzen, 1966a). However, the problem has been raised that not all of these interactions are quite mutualistic. Some organisms (ants, birds, etc.) may take advantage of the situation and become parasites of these mutualisms (Yu, 2001). In fact, if one of the organisms that is itself involved in the mutualism takes advantage, then what we have is no longer a mutualism, but a case of parasitism (T. P. C. H. S. Young, Lynne A. Isbell, 1996).

Some ant species behave as true mutualists, for example Neotropical *P. ferruginea* (Janzen, 1966a), while others behave as parasites of the mutualism at varying levels. *Crematogaster mimosae* defends *A. drepanolobium* from herbivores, but also farms adult scale insects that may have a detrimental effect on the acacia. *Crematogaster sjostedti*, on the other hand, farms harmful scale insects, while at the same time effectively ignoring attacking herbivores (T. Y. a. M. Stanton, 1999; T. P. C. H. S. Young, Lynne A. Isbell, 1996). Also, the generalist (or generalist-similar) ant species discussed, *Camponotus planatus*, is a clear parasite of the ant-plant mutualism (Janzen, 1975).

To conclude, the interactions between ants and plants can indeed be a true mutualism, but often it borders on parasitism, and can even become fully parasitic in nature. It is notable that the plants do not seem to parasitize the mutualism with ants, but they are capable of rebalancing it through the use of exclusion filters and other tactics e.g., the ability of some plants to use absorptive inner wall structures to draw nutrients out of trash piles left by ants (Rickson, 1979), and the presence of ant-repellent chemicals in the floral tissues of New-world *Acacia* which prevent co-option of the plant-pollinator mutualism by plant-ants (Ghazoul, 2001). Further research into the behaviors of different taxa of *Pseudomyrmex* in Central America, as well as study of possible exclusion filters at work in *Acacia*, perhaps in regards to site selection by founder queens, would provide much greater insight into the nature of the ant-acacia interaction. We may even find the need to redefine the nature of even some of the most commonly sited mutualisms.

WORKS CITED

Becerra, J. X. I., D. Lawrence Venable. 1989. Extrafloral Nectaries: A defense against Ant-Homoptera Mutualisms? Oikos 55:276-279.

Brouat, C., Nelly Carcia, Claude Andary, Doyle McKey. 2001. Plant lock and ant key: pairwise coevolution of an exclusion filter in an ant-plant mutualism. Biological Sciences 268:2131-2141.

Brown, W. L. 1960. Ants, Acacias, and Browsing Mammals. Ecology 41:587-592.

Espelie, K. E., and Henry R. Hermann. 1988. Congruent Cuticular Hydrocarbons: Biochemical Convergence of a Social Wasp, an Ant, and a Host Plant. Biochemical Systematics and Ecology 16:505-508.

Frederickson, M. E. 2005. Ant species confer different partner benefits on two neotropical myrmecophytes. Oecologia 143:387-395.

Ghazoul, J. 2001. Can floral repellents pre-empt potential ant-plant conflicts? Ecology Letters 4:4:295-299.

Janzen, D. H. 1966a. Coevolution of Mutualism Between Ants and Acacias in Central America. Evolution 20:249-275.

—. 1966b. Fire, Vegetation Structure, and the Ant X Acacia Interaction in Central America. Ecology 48:26-35.

—. 1969. Birds and the Ant x Acacia Interaction in Central America, with Notes on Birds and Other Myrmecophytes. The Condor 71:240-258.

—. 1975. Pseudomyrmex nigropilosa: A Parasite of a Mutualism. Science 188:936-937.

Knox, R. B., J. Kendrick, P. Bernhardt, R. Marginson, G. Beresford, I. Baker, H. G. Baker. 1985. Extrafloral Nectaries as Adaptations for Bird Pollination in Acacia terminalis. American Journal of Botany 72:1185-1196.

Letourneau, D. K. 1990. Code of Ant-Plant Mutualism Broken by Parasite. Science 248:215-217.

Raine, N. E. N. G., Iain J. Macfadyen, Gareth K. Scrivner, Graham N. Stone. 2004. Guards and thieves: antagonistic interactions between two ant species coexisting on the same ant-plant. Ecological Entomology 29:345-353.

Rickson, F. R. (1979). Absorption of animal tissue breakdown products into a plant stem-the feeding of a plant by ants. Am J Bot, 66:87-90.

Stanton, M. L., T.M. Palmer, T.P. Young. 2002. Competition-Colonization Trade-Offs in a Guild of African Acacia-Ants. Ecological Monographs 27:347-363.

Stanton, T. Y. a. M. 1999. Thorny Relationships. Natural History 108:28-31.

Stapley, L. 1998. The Interaction of Thorns and Symbiotic Ants as an Effective Defense Mechanism of Swollen-thorn Acacias. Oecologia 115:401-405.

Young, B. E., Michael Kaspari, Thomas E. Martin. 1990. Species-Specific Nest Site Selection by Birds in Ant-Acacia Trees. Biotropica 22:310-315.

Young, T. P. C. H. S., Lynne A. Isbell. 1996. Ants on swollen-thorn acacias: species coexistence in a simple system. Oecologia 109:98-107.

Yu, D. W. 2001. Parasites of Mutualisms. Biological Journal of the Linnean Society 72:529-546.