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Cheating the cheater: domatia loss minimizes the effects of ant castration in an Amazonian ant-plant

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Abstract We studied the relationship between *Hirtella myrmecophila* (Chrysobalanaceae), a common but little-studied Amazonian ant-plant that produces leaf-pouches as domatia, and its obligate ant partner, *Allomerus octoarticulatus*. Field observations revealed that *H. myrmecophila* drops domatia from older leaves, a characteristic that is unique among myrmecophytes. The physiological mechanism for abortion of domatia is currently unknown, but this characteristic allows for the existence, within the same plant, of branches with and without ants. Older branches generally bear only old leaves with no domatia and therefore have no ants, whereas younger branches have leaves of various ages. Ants forage mainly on new leaves, and experimental removal of ants showed that *A. octoarticulatus* is crucial for defense of these leaves against insect herbivores. However, *A. octoarticulatus* also acts as a castration parasite, severing the plant's inflorescences. Mature flowers and fruits were only found on older branches with no ants, and flower production was 8 times greater on plants whose ants were experimentally removed than on control plants. Given the reproductive costs inflicted by its mutualistic partner, we suggest that abortion of domatia is a strategy developed by *H. myrmecophila* to minimize the effects of cheating by *A. octoarticulatus*. These results support the view that evolutionary conflicts of interest between mutualistic species often impose selection for cheating on the partner, as well as for mechanisms to retaliate or to prevent super-exploitation. Opposing selection pressures, operating independently on the two partners, probably help to maintain the evolutionary stability of this mutualistic relationship.

Keywords *Allomerus* · Myrmecophytes · Mutualism · *Hirtella* · Herbivory

Introduction

Myrmecophytes, also known as ant-plants, are plants that have evolved obligate, mutualistic relationships with ants (Janzen 1966; Beattie 1985; Benson 1985; Davidson and McKey 1993). To house ants, these plants have evolved special hollow structures, known as domatia, in which ants nest (Janzen 1966; Beattie 1985; Benson 1985). Many ant-plants also provide food to their associated ants, in the form of nectar or food bodies (Janzen 1966; Baudoin 1975; Janzen 1975; O'Dowd 1980; Beattie 1985; Vasconcelos 1991). In exchange, ants often protect plants against herbivores (Janzen 1966; McKey 1984; Benson 1985; Vasconcelos 1991; Davidson and McKey 1993; Fonseca 1994; Federle et al. 1998), against encroaching vines and competing plants (Janzen 1966; Benson 1985; Davidson and McKey 1993; Federle et al. 1998), or provide nutrients essential for plant growth (Janzen 1966; Treseder et al. 1995). However, not all associated ants are mutualistic. Some ant species act like parasites by utilizing domatia and food rewards without providing benefits (Janzen 1975; McKey 1984; Gaume and McKey 1999), while others prune the reproductive or vegetative structures of their host-plants, thus negatively affecting plant growth and reproduction (Yu and Pierce 1998; Stanton et al. 1999; Yu 2001).

Among ant species protecting myrmecophytes from herbivores (Vasconcelos 1991; Davidson and McKey 1993; Fonseca 1994), many do not forage or nest off their hosts, and for these species colony growth and reproductive success depend strongly on host-plant growth (Fonseca 1993, 1999). However, ant-plants can theoretically control the production of domatia, maintaining the available space for the colony at an optimum size that better reflects the plants' interest in terms of defense allocation (Fonseca 1993). If the plant's allocation to domatia is not the optimal solution for the ants, the inter-

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ests of the two partners are in conflict (Fonseca 1999), and cheating – the use of mutualistic resources or services without providing any benefits in return – can evolve.

This study focuses on the relationship between *Hirtella myrmecophila* (Chrysobalanaceae), a common but little-studied Amazonian ant-plant that produces leaf-pouches as domatia, and its obligate ant partner, *Allomerus octoarticulatus*. We begin by showing that *H. myrmecophila* loses its domatia from older leaves. We then analyzed the effects of *A. octoarticulatus* against plant herbivores and on plant reproduction. Given the reproductive costs incurred by its mutualistic partner, we suggest that abscission of domatia is a strategy developed by *H. myrmecophila* to minimize the effects of cheating by *A. octoarticulatus*.

Materials and methods

Study area

The study was conducted at an 800-ha forest preserve, run by the Biological Dynamics of Forest Fragments Project (a collaborative project between INPA – the Brazilian National Research Institute for the Amazon – and the Smithsonian Institution). This preserve is situated about 70 km north of Manaus (2°25'S, 59°48'W), within an area of approximately 500,000 ha of relatively undisturbed, upland (*terra-firme*) Amazonian rain forest that is being developed by the Manaus Free Trade Zone Authority (SUFRAMA). The preserve is on moderately rugged terrain, dissected by small creeks, and lies at an elevation of 50–100 m. Canopy height of forest trees is about 35 m, with some emergent trees reaching up to 50 m. The understory is relatively open and characterized by an abundance of stemless palms. Precipitation in Manaus averages 2,100 mm annually and varies seasonally, with a rainy period between November and May and a dry period between June and October (Ribeiro 1976).

Study species

The genus *Hirtella* (Chrysobalanaceae) has 98 species, of which only 7 are myrmecophytic (Prance 1972). *H. myrmecophila* is a small (<10 m) understory tree commonly found in non-flooded forests of the central Amazon. It produces ant cavities (domatia) at the base of the leaves, but these domatia are subsequently lost as the leaf ages (Fig. 1). The physiological mechanism that promotes the abortion of domatia is currently unknown. The domatia of *H. myrmecophila* are highly vascularized, and are irrigated by secondary veins independently from the remaining leaf lamina. Therefore, disruption of sap flux to those secondary veins could cause the necrosis of the domatia without affecting the leaf lamina.

H. myrmecophila reproduces year-round. It has fasciculate inflorescences, 1–3.5 cm long, which are produced usually at the tip of the branches (Fig. 1). In mature forests near Manaus (Brazil), this myrmecophyte has only one obligate associate, the ant *A. octoarticulatus*. Of 600 plants inspected (Izzo 2001), 583 (97.16%) hosted colonies of *A. octoarticulatus*, 12 plants were uninhabited by ants, and the remaining 5 plants housed either *Crematogaster limata parvibotica* ($n=4$) or *Azteca* sp. ($n=1$). The last two species, however, were never found nesting in the plant, but only tending scale insects (Izzo 2001).

A. octoarticulatus is a tiny ant (<2 mm), relative of the fire-ants, which lives exclusively in myrmecophytes, including also *Duroia saccifera* (Rubiaceae) and *H. physophora* in central Amazonia (Fonseca 1999; Ribeiro et al. 1999). A taxonomic revision of the genus *Allomerus* is urgently needed, as in many cases the

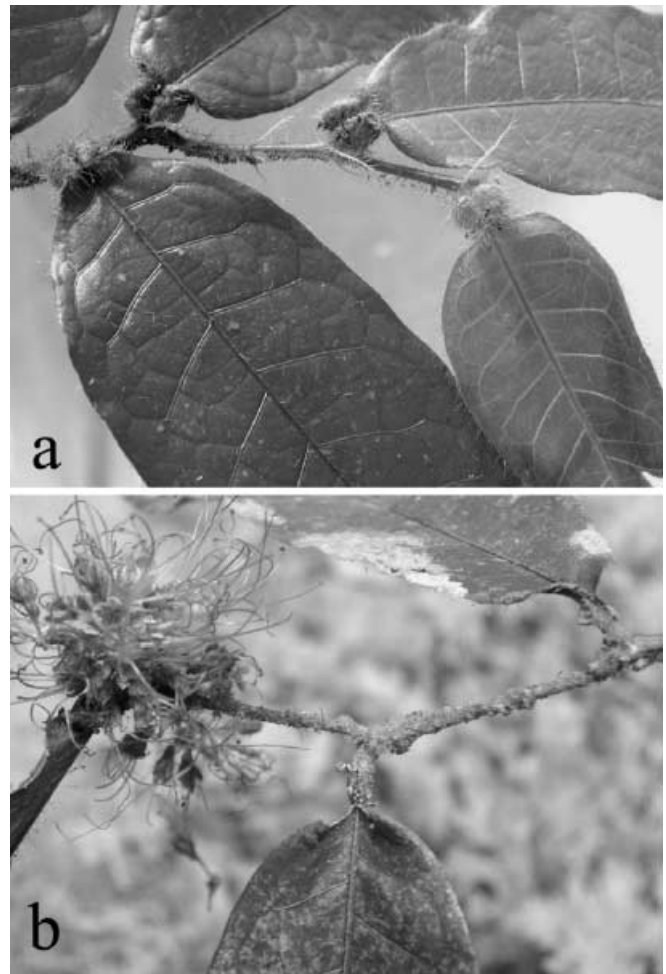


Fig. 1 **a** Young branch of the ant-plant, *Hirtella myrmecophila*, containing new and mature leaves with domatia (leaf pouches located at the base of the leaf, where associated *Allomerus octoarticulatus* ants nest). **b** On the same plant, older branch with leaves where domatia were aborted (right), and an inflorescence (left)

species delimitations are unresolved. For instance, in our study site about 3% of the plants were occupied by *A. octoarticulatus* var. *septemarticulatus*, which is distinguished from *A. octoarticulatus* by the number of antennal segments (seven in *septemarticulatus* and eight in *octoarticulatus* sensu stricto). Apart from this single difference in worker morphology, we have not found any other morphological, behavioral or ecological difference between the two species varieties, so we assume these to be a single species. In spite of that, all observations and experiments described below were performed with plants inhabited by *A. octoarticulatus* sensu stricto.

A. octoarticulatus does not tend scale insects and does not forage off its host-plant. Its major food source appears to be insects that venture onto the plant foliage. During field observations, we saw *A. octoarticulatus* attacking and carrying to the interior of the domatia several kinds of insects, including caterpillars, beetles, and Homoptera, as well as termites that we experimentally placed onto the leaf lamina. The predatory behavior of *A. octoarticulatus* is very similar to that of *A. decemarticulatus* (Dejean et al. 2001).

Distribution of foraging ants according to leaf age

We counted the number of ants foraging on the leaf surface in 4 leaves per plant, for a total of 57 randomly selected plants (1–2.5 m tall). These were instantaneous counts, performed during the day, once for each plant. In each plant, we selected one new expanding leaf, one mature leaf, and two old leaves (one from a branch containing only old leaves, and one from a branch with new and mature leaves). Old leaves were defined as mature leaves that had lost their domatia (Fig. 1b), or that were about to lose the domatia (in the latter case, the domatia was already in the process of necrosis and was not utilized by ants). In addition, old leaves, in contrast to mature leaves, were frequently covered by epiphylls. The term “old” was used here to emphasize that these leaves were older than mature leaves with domatia. Old leaves were generally not senescing leaves, since many of the old leaves we marked survived for over 1 year. Of 84 marked old leaves during the ant-removal experiment (see below), only 10 (11.9%) died after 18 months.

To remove the effects of leaf size, ant activity was expressed per unit of leaf area (workers per 10 cm² of leaf) rather than per leaf. Leaf area was measured using a transparent plastic grid with a precision of 0.25 cm².

Ant-removal experiment

We selected 40 *H. myrmecophila* trees 1–2.5 m high. This size was chosen to facilitate access to all branches. The plants were assigned randomly into two treatments: ant removal by application of organophosphate insecticide Malathion (Indol do Brasil) inside all domatia, or control (plants whose ants were maintained). In total, four plants were lost during the experiment to natural mortality, e.g. that resulting from treefalls. There were no initial differences in total leaf numbers of control and treatment plants (mean±SE: control=84.5±6.7; treatment=85.2±8.0). Production of new leaves and flowers was recorded monthly during a 9-month period. At the end of that period, we recorded the total number of leaves per plant. These data were used to calculate the percent leaf increment per plant as: $[(N_f/N_i)-1]*100$, where N_i is the initial number of leaves and N_f is the number of leaves 9 months after the beginning of the experiment.

Rates of leaf herbivory (percent leaf area damaged per month) were recorded for new, expanding leaves for a period of 1 month, and for mature and old leaves for a 2-month period. In each plant, we randomly selected three leaves per age category. New leaves were those produced after the beginning of the experiment. For each leaf we recorded, monthly, the total leaf area, and the area damaged. Differences in herbivory rates between control and treatment plants were assessed using the Mann-Whitney *U*-test. A separate test was done for each leaf category. Since the same hypothesis was being tested several times, probabilities were corrected using the Bonferroni procedure. All analyses were done using SYSTAT (Wilkinson 1996).

Effects on plant reproduction

To further assess the effects of *A. octoarticulatus* on plant reproduction, we conducted two experiments. First, we selected 16 trees that possessed undamaged young inflorescences on branches with ants. From one branch we removed, using insecticide, all ants from the most distal three leaves, which were then isolated from the remaining leaves with Tanglefoot (The Tanglefoot Company, Mich.). Another branch from the same plant was marked as a control, and remained unmanipulated.

The second experiment took advantage of the fact that in *H. myrmecophila* two types of branches are found. Younger branches (as those used in the above described experiment) have ants, whereas older branches bearing only old leaves do not (see Results). In each of 11 randomly selected trees, we tied 1 old branch with at least 1 young inflorescence to a nearby young branch with

no flowers. As a control, we tied together two old branches, one with a young inflorescence and one without any flowers.

In both experiments, we followed the fate of each marked inflorescence for 1 month, recording if the inflorescence died or became a fully formed (mature) inflorescence.

Results

Distribution of foraging ants according to leaf age and branch type

Ant activity was highly concentrated on new, expanding leaves; the average number of foraging ants per unit of leaf area was an order of magnitude greater on newly expanding leaves than on mature (Wilcoxon signed ranks test $Z=6.6$; $P<0.001$) or old leaves ($Z=6.6$; $P<0.001$; Table 1). We never found foraging ants on old leaves in branches containing only old leaves, whereas a few ants were found on old leaves from branches containing also new and mature leaves (Table 1). Therefore, within the same plant, there were branches with and without ants. The proportion of branches with and without ants was found to be variable among trees, probably due to tree age and environmental factors; however, on average 65% (SE=2.2; $n=42$ plants) of the branches from a given tree housed ants in all or most of their leaves, whereas 35% of the branches bore only old leaves lacking ants.

Ant-removal experiment

Experimental removal of ants from entire individuals of *H. myrmecophila* resulted in significantly higher herbivory rates, particularly for newly expanding leaves (Table 2). New leaves not protected by ants were heavily attacked by leaf-eating insects, especially caterpillars, beetles, and grasshoppers. Levels of herbivore damage on mature and old leaves were very low and did not differ between control and treatment plants (Table 2).

Table 1 Effects of leaf type and branch type on the distribution of foraging ants (*Allomerus octoarticulatus*) in the ant-plant *Hirtella myrmecophila*. Younger branches were those that presented leaves of different ages, most of which had domatia. Older branches were those that contained only old leaves without domatia. No ants were found in old leaves from older branches, whereas in younger branches ant activity was highly concentrated on new, expanding leaves. Values represent means±SE ($n=57$ plants)

Branch type	Leaf type	Abundance of foraging ants (number per 10 cm ² of leaf surface)
Young	New (expanding) – with domatia	5.48±0.79
	Mature – with domatia	0.11±0.02
	Old – without domatia	0.01±0.01
Old	Old – without domatia	0

Table 2 Effects of ant removal on leaf and flower production, and on herbivory rates (% total leaf area damaged in 1 month) for new, mature, and old leaves of *Hirtella myrmecophila*. Ant removal significantly increased herbivory in new leaves, negatively affect-

ed plant growth, but increased flower production. Values represent means \pm SE. For treatment plants $n=19$ in all cases, and for control plants (ant-maintained) $n=19$ for data on herbivory rates and $n=17$ for the remaining variables

Variable	Control (with ants)	Treatment (ants removed)	U-test statistic	P
% leaf area damaged in 1 month – new leaves	1.17 \pm 0.77	54.22 \pm 6.58	3.0	<0.001*
% leaf area damaged in 1 month – mature leaves	0.06 \pm 0.02	1.20 \pm 0.60	117.0	0.18*
% leaf area damaged in 1 month – old leaves	0.40 \pm 0.13	0.25 \pm 0.09	189.5	1.00*
% of new leaves that did not reach maturity ^a	1.39 \pm 0.89	56.96 \pm 5.86	10.0	<0.001
Number of new leaves produced in 9 months	17.06 \pm 1.96	6.79 \pm 1.06	285.0	<0.001
% leaf increment in 9 months	11.89 \pm 3.76	-5.16 \pm 2.88	263.5	0.001
Number of inflorescences produced in 9 months	0.88 \pm 0.39	6.74 \pm 2.31	87.0	0.013

*Bonferroni-adjusted probability

^aAborted or completely eaten by herbivores 1 month after emergence

Treatment plants produced threefold fewer new leaves than did control plants within a period of 9 months (Table 2). Moreover, 57% of the few leaves produced by treatment plants were completely lost to herbivores 1 month after emergence, compared to just 1.4% of those from control plants (Table 2). Due to both lower rates of leaf production and elevated rates of herbivore damage, ant-removal plants exhibited negative growth over the course of the experiment, whereas numbers of leaves increased by 12% on average in control plants (Table 2). Removal of ants also dramatically affected flower production. Despite suffering more herbivory, treatment plants produced an average of 8 times more flowers (inflorescences) than did control plants (Table 2).

Effects on plant reproduction

The presence of inflorescences on branches with ants always elicited strong recruitment of ants. Recently formed inflorescences were always covered with ants, and within 2 or 3 days became dry and died. Due to the small size of *A. octoarticulatus* and its sensibility to proximity of a human observer, we were not able to directly observe and describe the castration behavior in detail. However, results from our field observations and experiments provide strong indirect evidence for the role of *A. octoarticulatus* as a castration parasite of *H. myrmecophila*. First, we never found fully formed flowers or fruits in young branches of ant-inhabited plants, whereas 49.1% (± 4.9 SE, $n=42$) of the old branches of these same plants bore mature flowers or fruits. Second, we frequently found young, dead flowers on young branches (with ants) but not on old ones (without ants) (10.6 \pm 2.0% of young branches with at least 1 dead inflorescence vs 1.8 \pm 0.9% of old branches; Wilcoxon signed ranks test: $Z=4.2$; $P<0.001$). Third, when young inflorescences were protected from ants by removing ants from the three most distal leaves, all but one inflorescence survived, whereas on the branches with ants all inflorescences died ($\chi^2=24.6$; $P<0.001$). Finally, when we tied one branch without ants and with at least one young inflorescence to a branch with ants, the ants destroyed all

inflorescences. In contrast, on control branches, all inflorescences survived ($\chi^2=18.2$; $P<0.001$).

Discussion

Our results suggest that while *A. octoarticulatus* protects *H. myrmecophila* from insect herbivory, it also lowers its fitness by castrating flowers. In response, *H. myrmecophila* appears to abort domatia in order to force ant abandonment from older branches and therefore flowering on these same branches. We now discuss each of these conclusions and their implications for mutualism theories.

The role of *Allomerus* in plant defense

Experimental removal of *A. octoarticulatus* resulted in strong herbivore damage to *H. myrmecophila* young leaves, indicating that young leaves rely heavily on ants for defense. Mature leaves and old leaves are not defended by ants, since virtually no damage was recorded after ant removal (Table 2). The number of patrolling ants on young, expanding leaves was an order of magnitude greater than on mature leaves (Table 1). This difference cannot be attributed to differences in nest location, since *A. octoarticulatus* occupied domatia of young and mature leaves equally. A recent study with *Leonardoxa africana* shows that associated *Petalomyrmex* ants are attracted to young leaves by leaf volatiles (Brouat et al. 2000), but if a similar phenomenon occurs in *H. myrmecophila* remains to be seen.

In general, our results support earlier findings with an African (*Leonardoxa africana*) (McKey 1984) and an Asian (*Crypteronia griffithii*) (Moog et al. 1998) myrmecophyte. In these plants, contrasting with many other ant-plants studied so far (e.g., Janzen 1966; Vasconcelos 1991; Fonseca 1994), chemical defenses have not been completely replaced by biotic (ant) defenses (McKey 1984; Moog et al. 1998). Rather, biotic and chemical/mechanical defenses coexist, each restricted to leaves of a different age class. Why do some myrmecophytes rely completely on biotic defenses whereas others do

not? Possibly, for ant-plants whose leaves are very long-lived, the cost of maintaining a large worker force of ants throughout the life of the leaf is too high relative to the cost of providing leaves with permanent chemical or mechanical protection. In this case, a trade-off from biotic to chemical and mechanical defenses as the leaf ages is expected (McKey 1984, 1988). *H. myrmecophila*, like *L. africana* and *Crypteronia griffithii*, also has long-lived leaves (>2 years; T.J. Izzo, unpublished results). However, leaf longevity may not be the only factor involved. Studies with *Tachigali myrmecophila*, an Amazonian ant-plant whose leaves live more than 6 years, do not support the trade-off model of chemical and ant defenses (Fonseca 1994).

The extremely high rates of herbivory observed on new *H. myrmecophila* leaves whose ants were removed, coupled with the fact that ant-removed plants were not able to replace the leaves lost to herbivores, suggest that these plants are likely to die if not recolonized by ants.

Allomerus as a castration parasite of *Hirtella myrmecophila*

Mature flowers and fruits were only found in older branches without ants, suggesting that either: (1) *A. octoarticulatus* destroys the reproductive structures of its host-plant, or (2) there is a physiological difference between branches with and without ants and, for some reason, those with ants discontinue flower development. Our experiments indicate that there are no physiological differences between branches with and without ants, but rather that *A. octoarticulatus* only destroy flowers from the branches they inhabit. Therefore, *A. octoarticulatus* castrates its host-plant. This behavior is also seen in its congener *A. demerarae* which lives in *Cordia nodosa* (Boraginaceae) (Yu and Pierce 1998; Yu 2001).

Destruction of *H. myrmecophila* flowers by *A. octoarticulatus* always occurred very early in flower development. The ants attacked floral buds immediately after they were produced. In that sense, the energetic loss to the plant is less than if attacks occurred only after flowers had matured or after fruit set. This castration behavior is probably beneficial for the ant colony, because it increases nesting space (Yu and Pierce 1998; Yu 2001), given the likely trade-off between plant growth and reproduction (Baudoin 1975; Clay 1990; Yu and Pierce 1998; Stanton et al. 1999; Kover 2000; Yu 2001). Because both leaves and flowers of *H. myrmecophila* are produced at the branch tips (Fig. 1), a given branch may not be able to produce the two structures concomitantly.

In the *Cordia-Allomerus* system, as in other ant-plant systems in which ant parasitism is recorded, plant populations persist because other obligate plant-ant species that do not affect plant reproduction inhabit some plants (Janzen 1975; McKey 1984; Yu and Pierce 1998; Gaume and McKey 1999; Yu 2001). However, in the *Hirtella-Allomerus* system, only one ant species inhabits the plant. Although *A. octoarticulatus* is crucial for the de-

fense of young *H. myrmecophila* leaves, it also interferes with plant reproduction. Therefore, the abortion of domatia from old leaves – which do not rely on ants for defense – appears to be a strategy evolved by *H. myrmecophila* in order to “cheat the cheater”. With this strategy, the plant reduces the reproductive losses caused by its mutualistic partner while maintaining the benefits and stability of the association. Alternatively, domatia abortion could be simply a response to damage caused by pathogens, herbivores, or an ant-predator (e.g., Federle et al. 1999). However, this hypothesis appears unlikely. During our field observations, we never detected any organism causing this type of damage. Moreover, experimental removal of ants did not cause subsequent necrosis and abortion of domatia.

We have not observed abortion of domatia in *D. saccifera* or in *H. physophora*, even though these plants are also associated with *A. octoarticulatus*. We do not have any observations on flowering and fruiting in *D. saccifera*, whose height at maturity (>10 m) makes it difficult to monitor its reproductive phenology. However, preliminary observations with *H. physophora* reveal that inflorescences are most frequently produced on the tree trunk, where *Allomerus* ants do not forage. In addition, the petioles of the inflorescences of *H. physophora* are thicker and more densely covered with trichomes than those of *H. myrmecophila*, which may render them less susceptible to ant damage. These data suggest that flower morphology and flower position within the plant may be important determinants of whether or not plants are susceptible to ant castration. Although phylogenetic studies with myrmecophytic *Hirtella* are clearly needed, our preliminary observations with *H. physophora* indicate that domatia loss is not a common trait among all the species in the genus, and thus probably originated secondarily in *H. myrmecophila*.

Implications for the evolution of mutualisms

To our knowledge, this is the first study to demonstrate empirically that by modifying their morphology, plants can avoid castration by associated ants. Prior studies have suggested this could be the case, though it was observed in only a few individuals and intra-individual expression of the trait was highly variable (Yu and Pierce 1998). In contrast, the abortion of domatia in *H. myrmecophila* as a leaf ages appears to be not only consistent within an individual's lifetime, but also characteristic of the species as whole.

The *Hirtella-Allomerus* system resembles other species-specific mutualisms where mechanisms have evolved to enhance benefits of association and reduce costs due to cheating, and where such mechanisms promote the stability of the relationship (Tyre and Addicott 1993; Pellmyr and Huth 1994; West and Herre 1994; Pellmyr et al. 1996). In mutualistic systems involving *Ficus* and *Yucca* and their respective pollinators, the plants “pay” their specific pollinators with potentially vi-

able seeds for the growing larvae, in exchange for the pollination services provided by adult female insects. Therefore, the decrease in plant reproductive success is counter-balanced immediately by the pollination service (Tyre and Addicott 1993; Pellmyr and Huth 1994; West and Herre 1994; Pellmyr et al. 1996). In contrast, *H. myrmecophila* suffers a direct loss in reproductive success in exchange for an indirect increase in fitness obtained through protection against herbivores.

Our study shows the importance of herbivory as a key factor behind the evolution of myrmecophytism in *H. myrmecophila*, and probably also in many other ant-plants. It also reinforces the view that, in mutualistic systems, there is often a conflict of interests between partners, and that a mechanism to prevent cheating is necessary to stabilize the system.

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