Natural History Note
Conflict over Reproduction in an Ant-Plant Symbiosis: Why Allomerus octoarticulatus Ants Sterilize Cordia nodosa Trees

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Abstract: The evolutionary stability of mutualism is thought to depend on how well the fitness interests of partners are aligned. Because most ant-myrmecophyte mutualisms are persistent and horizontally transmitted, partners share an interest in growth but not in reproduction. Resources invested in reproduction are unavailable for growth, giving rise to a conflict of interest between partners. I investigated whether this explains why Allomerus octoarticulatus ants sterilize Cordia nodosa trees. Allomerus octoarticulatus nests in the hollow stem domatia of C. nodosa. Workers protect C. nodosa leaves against herbivores but destroy inflorescences. Using C. nodosa trees with Azteca ants, which do not sterilize their hosts, I cut inflorescences off trees to simulate sterilization by A. octoarticulatus. Sterilized C. nodosa grew faster than control trees, providing evidence for a trade-off between growth and reproduction. Allomerus octoarticulatus manipulates this trade-off to its advantage; sterilized trees produce more domatia and can house larger, more fecund colonies.

Keywords: ant-plant, castration, partner fidelity feedback, myrmecophyte, reciprocity, trade-off.

Introduction

Mutualisms are common in nature, but theoreticians have struggled to explain their evolution and persistence. Instead of mutualists, natural selection should favor cheaters that take the benefits of cooperation without paying the cost of reciprocating. Many models have been proposed to explain the evolution of cooperation, although most have focused on cooperation within a species. Sachs et al. (2004) grouped these models into three classes: shared genes, by-product benefits, and directed reciprocation. The evolution of mutualism between two species cannot be explained by shared genes (i.e., kin selection) because the partners are not close relatives. Models that invoke by-product benefits hinge on there being no cost to cooperation and hence no incentive to cheat. Only directed reciprocation can explain how an individual of one species evolves to benefit an individual of another species at some cost to itself.

Trivers (1971) and Axelrod and Hamilton (1981) developed the idea of directed reciprocation by drawing an analogy between mutualism and the iterated prisoner’s dilemma. According to our current understanding of directed reciprocation, mutualism can evolve if (1) individuals interact repeatedly, such that the benefits provided by individual A to individual B eventually feed back to individual A, a mechanism called partner fidelity feedback, or (2) individuals cooperate with cooperative individuals but do not cooperate with noncooperative individuals, a mechanism called partner choice (Bull and Rice 1991; Sachs et al. 2004; Foster and Wenseleers 2006). These mechanisms may work together or separately to promote the evolutionary stability of mutualism and prevent cheating.

Symbiotic interactions between ants and plants are classic examples of mutualism (e.g., Janzen 1966) and good candidates for partner fidelity feedback (Sachs et al. 2004). Ant-plants, or myrmecophytes, house ants in specialized structures called domatia. Often, an ant queen colonizes a myrmecophytic plant when the plant is young or small, and the plant and the ant colony grow together for many years, during which time the relationship is exclusive. Positive feedback occurs between ant colony and plant growth (Frederickson and Gordon, forthcoming). Ant workers defend the plant against herbivores or encroaching vegetation and, in so doing, promote plant growth. Myrmecophytic plants produce domatia and often food bodies as they grow, increasing nesting space and food for the ant colony and hence promoting ant colony growth. Thus, the benefits an ant colony provides to its plant feed back to the ant colony and vice versa. In such a system, natural selection favors mutualism and not cheating because an individual (or colony) that fails to cooperate reduces its own fitness. If ant workers cheat and do not protect their host plant, the plant does not grow and does not produce the...
Partner fidelity feedback is strongest when all the components of individual fitness are interdependent between partners, that is, when the survival, growth, and reproduction of one partner depend on the survival, growth, and reproduction of the other. However, this is rarely the case in mutualisms (Herre et al. 1999; Wilkinson and Sherratt 2001). In ant-plant mutualisms and many others, horizontal transmission gives rise to a conflict between the fitness interests of partners. When plants and ant colonies are small, the resources they acquire are invested in growth, and the fitness interests of partners are aligned via partner fidelity feedback because the growth of one partner facilitates the growth of the other. However, as plants and ant colonies grow together and become large, they begin to invest in reproduction. Because there is no guarantee that their offspring will associate in the next generation, neither partner gains from the reproduction of the other. In horizontally transmitted mutualisms, partners depend on the successful reproduction of some partners in the population but not on the reproduction of the particular individuals with which they interact. Moreover, resources invested in reproduction are unavailable for growth and thus impose a cost and provide no benefit to a mutualistic partner.

I investigated the conflict of interest over reproduction that occurs between the ant species *Allomerus octoarticulatus* and the myrmecophytic plant *Cordia nodosa*. *Allomerus octoarticulatus* protects the leaves of *C. nodosa* against herbivores, as do the other ant species that nest in *C. nodosa* (Frederickson 2005). However, unlike the other ant inhabitants of *C. nodosa*, *A. octoarticulatus* destroys *C. nodosa* floral buds and flowers (fig. 1), which reduces fruit production and, hence, plant fitness (Yu and Pierce 1998). Although this behavior was termed plant castration by Yu and Pierce (1998), here I use the term plant sterilization because it is more general and reduces confusion; the ants destroy both male and female floral parts.

*Allomerus octoarticulatus* is one of three ant species that have been shown to destroy the reproductive structures of their host plants; the others are *Crematogaster nigriceps* (Stanton et al. 1999) and *Crematogaster dohrni* (Gaume et al. 2005). Stanton et al. (1999) proposed that *C. nigriceps* prunes and sterilizes *Acacia drepanolobium* to reduce contacts with neighboring trees occupied by competitively dominant ants. However, an earlier study of the same system suggested that sterilization might also result in the reallocation of resources from reproduction to growth (Young et al. 1997). Yu and Pierce (1998) developed this idea more fully and hypothesized that *A. octoarticulatus* sterilizes *C. nodosa* so that the plant continues to invest resources in growth, resources that would otherwise be diverted to reproduction. Ants living in myrmecophytes depend on plant growth and domatia production to grow their colonies. Thus, ants that sterilize their hosts should have faster-growing and more fecund colonies and higher fitness. Similar reasoning has been used to explain why *A. octoarticulatus* sterilizes *Hirtella myrmecophila* (Izzo and Vasconcelos 2002) and possibly why *C. dohrni* sterilizes *Humboldtia brunonis* (Gaume et al. 2005). However, the hypothesis that sterilization increases domatia production has never been tested experimentally. I tested this hypothesis by comparing the growth rates of artificially sterilized and control *C. nodosa* trees. Using *C. nodosa* with colonies of *Azteca* ants, which do not sterilize their host plants, I destroyed inflorescences and compared domatia production between experimental (inflorescences cut) and control (inflorescences not cut) trees.
Methods

This study was conducted at the Los Amigos Research Center (12°34'S, 70°05'W; elevation ~270 m), located at the junction of the Madre de Dios and Los Amigos rivers in Amazonian Peru. Surrounding the research center is the Los Amigos conservation concession, which comprises 146,000 ha of primary tropical rainforest on a mixture of upland terraces and floodplains. Annual rainfall at Los Amigos is between 2,700 and 3,000 mm, with more than 80% of the precipitation falling during the October–April wet season (Pitman 2008). Mean monthly temperatures range from 21°C to 26°C (Pitman 2008).

At Los Amigos and elsewhere, *Cordia nodosa* associates with several ant species. The most common ant associate is *Allomerus octoarticulatus* (previously described as *Allomerus demerarae*; see Yu and Pierce 1998; Yu et al. 2001, 2004). *Cordia nodosa* also associates with at least three species in the genus *Azteca*. In this study, I identified *Azteca* ants to genus only because species are difficult to distinguish based on worker morphology, and I did not observe reproductive. *Myrmelachista schumanni* also colonizes *C. nodosa*, but colonies of this ant species are rare at Los Amigos. All these ant species found colonies independently and tend to colonize small *C. nodosa* trees (Frederickson and Gordon, forthcoming). There is little evidence that one ant colony ever invades and expels another colony that is already established on a plant (Frederickson 2005). However, if an ant colony dies, its host plant can be re-colonized by ants of the same or a different species (Frederickson and Gordon, forthcoming).

In southeastern Peru, *A. octoarticulatus* appears to be an obligate symbiont of *C. nodosa* in this region, it has been collected only from *C. nodosa* (Yu and Pierce 1998). However, this species specificity breaks down at larger geographic scales. In Brazil, ants identified as *A. octoarticulatus* have been collected from *Duroia saccifera*, *Hirtella mrymecophila*, *Hirtella physophora*, *Remejia physophora*, and *Tococa* spp. (Wheeler 1942; Fonseca 1999; Izzo and Vasconcelos 2002; Fernández 2007). Further work is needed to determine whether *A. octoarticulatus* is a single species or a complex of closely related species (Fernández 2007).

As in many other ant-myrmecophyte mutualisms, the ants defend *C. nodosa* against herbivores; *A. octoarticulatus*, *Azteca* spp., and *Myrmelachista schumanni* have all been shown to protect their host plants’ young leaves from phytophagous insects (Yu and Pierce 1998; Frederickson 2005). The ants depend on the plant for nesting space (i.e., domatia) and food. *Cordia nodosa* produces domatia—hollow swellings on otherwise slender branches—whether or not ants are present. Each time a *C. nodosa* tree grows a new shoot, it produces one domatium together with a whorl of new leaves. If the tree has ants, the colony quickly fills this new domatium with brood and workers. *Cordia nodosa* trees also produce food bodies on the surfaces of young leaves and shoots (Solano et al. 2005). Ants get additional food from the honeydew-producing scale insects (Hemiptera: Sternorhyncha: Coccoidea) they tend inside domatia. Because *C. nodosa* trees produce one domatium per internode as they grow (and lose domatia when branches senesce), the number of domatia on a tree is a good measure of plant size. The number of domatia also determines the amount of nesting space available to the ant colony.

In June–August 2007, I searched 2,107 m of trail at Los Amigos and numbered and tagged every *C. nodosa* tree that I saw. For each tree, I recorded the number of domatia, the type of ant occupant, if any, and the presence of flowers and fruit. A plant was considered to be occupied by ants if workers were observed on the plant. I compared the size and reproductive status of plants with different ant occupants using ANOVA and $\chi^2$ tests.

To test whether sterilization affects domatia production, I used 30 *C. nodosa* with the following characteristics: (1) each tree was occupied by a colony of *Azteca* ants, (2) each tree was producing flowers or fruit, and (3) the upper branches of each tree could be reached by standing on a 1.7-m ladder. Domatia were counted and individually marked with thin plastic-coated wires. Trees were matched according to size and then assigned randomly to either the experimental (inflorescences cut) or control (inflorescences not cut) treatment. The inflorescences were cut off trees in the experimental treatment roughly once a month for 4 months, beginning August 26–27, 2007. Inflorescences were cut at their peduncles using scissors. Severed inflorescences were left on leaves so that any ants on the inflorescences could return to their nest. Inflorescences were not cut. Every month, the number of domatia, inflorescences, and fruits were recorded for all trees in both treatments, and new domatia were marked with a different color of plastic-coated wire. The data were analyzed using paired t-tests. The number of fruits was square root transformed to improve normality.

Results

*Allomerus octoarticulatus* was the most abundant ant associate of *Cordia nodosa*, occupying 43.3% of the 120 plants in the survey; *Azteca* spp. occupied 34.2% of plants, 20.0% of plants did not have ants, and the remaining 2.5% of plants were occupied by unidentified ant species. No *Myrmelachista schumanni* colonies were found in the survey, although I have observed colonies of this species at other locations nearby.

Plant size and reproductive status depended on the presence and type of ants. Plants with ants were larger than plants without ants, and plants with *Azteca* spp. were
larger than plants with *A. octoarticulatus* (fig. 2; ANOVA; $F_{2,114} = 35.56$, $P < .0001$). None of the plants with *A. octoarticulatus* bore any flowers or fruits, while 68% of *C. nodosa* with *Azteca* spp. and 8% of *C. nodosa* without ants were producing either flowers or fruits ($\chi^2_{2,117} = 60.82$, $P < .0001$).

At the start of the sterilization experiment, trees in the experimental and control groups were nearly the same size (fig. 3; paired $t$-test: $t_{14} = 0.38$, $P = .71$). As expected, the experimental treatment significantly reduced fruit production. At the end of the experiment, trees in the experimental group had significantly fewer fruits than trees in the control group (mean ± SE: experimental 1.2 ± 0.88 fruits, control 4.8 ± 1.91 fruits; paired $t$-test: $t_{14} = 2.39$, $P = .03$).

Sterilization increased plant growth. Trees in the experimental group grew faster than trees in the control group (fig. 3; paired $t$-test: $t_{14} = 2.38$, $P = .03$). This difference in net growth rate was due to both the production of new domatia and the senescence of old domatia. In 4 months, *C. nodosa* trees in the control treatment produced an average (± 1 SE) of 14.3 ± 3.38 new domatia and lost 10.7 ± 4.08 old domatia, while trees in the experimental treatment produced 19.6 ± 4.77 new domatia and lost 4.00 ± 1.23 old domatia.

**Discussion**

Sterilizing *Cordia nodosa* increased domatia production and retention, as suggested by Yu and Pierce (1998). This result demonstrates that the allocation of resources by *C. nodosa* trees is subject to a trade-off between growth and reproduction. *Allomerus octoarticulatus* takes advantage of this trade-off, sterilizing *C. nodosa* before the plant can use valuable resources to produce fruits and seeds; the plant invests these resources in branches and domatia instead. At the end of the 4-month experiment, sterilized *C. nodosa* had 18% more domatia than control plants.

For an *A. octoarticulatus* colony, more domatia should mean higher fitness. There is a strong, positive correlation between the number of reproductives in an *A. octoarticulatus* colony and the number of domatia on the colony’s host plant (Yu and Pierce 1998; Frederickson 2006). Mortality of *A. octoarticulatus* queens during mating, dispersal, and colony founding is extremely high (~97%; Frederickson 2006). Hence, *A. octoarticulatus* colonies that produce more reproductives should have a better chance of having some queens survive and establish new colonies in the

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**Figure 2:** Size (mean ± 1 SE number of domatia) of *Cordia nodosa* trees; *AZ* = *Azteca* spp.; *AO* = *Allomerus octoarticulatus*; *NA* = no ants. Different letters indicate statistically significant differences according to Tukey post hoc tests ($P < .05$).

**Figure 3:** A, Size (mean ± 1 SE number of domatia) of *Cordia nodosa* trees at the beginning of the experiment. B, Growth rate (mean ± 1 SE net change in number of domatia) of *C. nodosa* trees in the experimental (inflorescences cut) and control (inflorescences not cut) treatments over the 4 months of the experiment (from August 26–27, 2007, to January 5–8, 2008). Different letters indicate statistically significant differences according to paired $t$-tests ($P < .05$).
next generation. Sterilization may also provide more food to the ant colony because *C. nodosa* produces food bodies on young leaves (Solano et al. 2005), and young leaves are produced together with new domatia. It should be noted that Yu and Pierce (1998) considered it unlikely that the ants get any food directly from the flowers and floral buds they attack; they stated that “most tissue simply desiccates and remains in place until it drops” (p. 377).

*Allomerus octoarticulatus* is extremely adept at sterilizing *C. nodosa*. In my survey, over two-thirds of plants with *Azteca* bore any flowers or fruits, yet not one *C. nodosa* with *A. octoarticulatus* bore any flowers or fruits. Most *A. octoarticulatus*–occupied *C. nodosa* were large enough to reproduce; more than 70% had at least 14 domatia, the minimum size at which *Azteca*-occupied *C. nodosa* produced flowers. Many *C. nodosa* bore signs of recent sterilization by *A. octoarticulatus*; their inflorescences had necrotic spots (fig. 1), the result of workers attacking floral buds (for a detailed description, see Yu and Pierce 1998).

When Yu and Pierce (1998) published their initial study of this system, they compared the growth rates of *A. octoarticulatus*– and *Azteca*-occupied *C. nodosa* to support the hypothesis that sterilization increases *C. nodosa* growth. They found that plants with *A. octoarticulatus*, which sterilize, grew faster than plants with *Azteca* spp., which do not. However, Frederickson (2005) found the opposite, albeit at a different site: *C. nodosa* grew faster with *Azteca* spp. than with *A. octoarticulatus*. At Los Amigos, *C. nodosa* were significantly larger with *Azteca* spp. than with *A. octoarticulatus* (fig. 2), again suggesting the former grow faster than the latter, although factors other than growth rate could also produce this difference. Collectively, these results imply that *A. octoarticulatus* and *Azteca* spp. differ in more ways than just their propensity to sterilize *C. nodosa* and also that there is significant geographic variation in this system, hence the need for a controlled experiment to test the effect of sterilization on plant growth. The conflicting results could be explained, for example, by geographic variation in the frequency of stem girdling by *Trachysomus* beetles. These beetles attack *C. nodosa* with *A. octoarticulatus* more often than they attack *C. nodosa* with *Azteca* spp., probably because *Azteca* spp. workers patrol *C. nodosa* trunks and deter herbivores from plant stems, while *A. octoarticulatus* workers do not (Yu and Pierce 1998; Frederickson 2005).

It is worth emphasizing two caveats to this study. First, it is well known that plants often respond differently to mechanical and insect damage, and it is possible that scissors do not effectively simulate the damage caused by *A. octoarticulatus* to *C. nodosa* inflorescences. Second, the experiment was conducted on *C. nodosa* trees occupied by *Azteca* spp., not on trees occupied by *A. octoarticulatus*. It would be interesting to investigate whether occupation or damage by *A. octoarticulatus* elicits a specific response from *C. nodosa* that differs from the plant’s response to mechanically severing its inflorescences. *Cordia nodosa* does respond differently to artificial defoliation than to sterilization; cutting leaves off *C. nodosa* with scissors to simulate herbivory results in greater mortality and reduced growth of the associated domatia and has no effect on subsequent rates of domatia production (Edwards et al. 2006).

Ant-associated plants sometimes produce floral ant repellents, presumably because ants would otherwise deter pollinators or reduce pollen viability (Willmer and Stone 1997; Ghazoul 2001; Nicklen and Wagner 2006). Ant interference with plant reproduction has largely been regarded as a by-product of selection for other ant traits. For example, Beattie et al. (1984) suggested that “the secretions of ants which function to combat microorganisms, by chance also incapacitate pollen grains” (p. 424). But ant interference in plant reproduction may be directly favored by natural selection more often than previously thought. Almost all ant–plant interactions are horizontally transmitted, although limited dispersal could bring about associations between ant and plant progeny similar to true vertical transmission. Furthermore, resource allocation trade-offs are widespread in plants, so a plant’s investment in ant rewards (extrafloral nectar, domatia, etc.) may often be negatively correlated with its investment in reproduction. This could explain why conflicts between ants and plants over plant reproduction are so commonly observed in nature.

Natural selection appears to have favored *A. octoarticulatus* colonies that sterilize *C. nodosa* because such colonies produce more queens and outcompete colonies that do not sterilize. *Allomerus octoarticulatus* sterilization of *C. nodosa* can be viewed as a tragedy of the commons (Rankin et al. 2007) because sterilization hurts the *A. octoarticulatus* population as a whole, despite individual gains. *Allomerus octoarticulatus* occupies between 40% and 80% of the *C. nodosa* trees in a population and reduces fruit production by 80%–100% on these trees (Yu and Pierce 1998; Dejean et al. 2004; Frederickson 2005; this study). Thus, sterilization by *A. octoarticulatus* substantially reduces the amount of fruits and seeds produced by a population of *C. nodosa*. It is not known whether seed production currently limits the number of *C. nodosa* recruiting into a population; other factors, such as space, could be limiting instead. However, the availability of nest sites does limit *A. octoarticulatus* (Frederickson 2006), so a decline in host plant numbers will lead to a decline in the population size of *A. octoarticulatus*. If *A. octoarticulatus* were the only ant associate of *C. nodosa*, the system would probably decline to extinction. Natural selection would increasingly favor
sterilization by \textit{A. octoarticulatus} colonies because such colonies would stand a better chance of having queens colonize increasingly scarce host plants. Eventually, \textit{A. octoarticulatus} colonies would reduce fruit production by \textit{C. nodosa} to zero, and no new host plants would recruit into the population, driving the \textit{A. octoarticulatus} population extinct. The presence of \textit{Azteca} spp. saves both the \textit{A. octoarticulatus} and \textit{C. nodosa} populations; theoretical and empirical work has investigated how \textit{Azteca} spp. and \textit{A. octoarticulatus} coexist in this system (Yu et al. 2001, 2004). An interesting avenue for future research would be to investigate why \textit{Azteca} colonies do not sterilize \textit{C. nodosa}; they would presumably reap the same benefits as \textit{A. octoarticulatus}.

\textit{Allomerus octoarticulatus} sterilization of \textit{C. nodosa} exemplifies the complex tug-of-war that occurs between partners in mutualisms. Traditionally, cooperation and cheating have been regarded as all-or-nothing strategies. In nature, however, organisms can rarely be neatly divided in this way, especially when persistent associations form between long-lived organisms whose fitness interests change over time. Is \textit{A. octoarticulatus} truly a parasite? It certainly reduces fruit production and prevents association with more beneficial ants (Yu and Pierce 1998). But it is difficult to know how occupancy by \textit{A. octoarticulatus} affects the lifetime fitness of \textit{C. nodosa}. On average, \textit{C. nodosa} trees live for 77 years, while \textit{A. octoarticulatus} and \textit{Azteca} spp. colonies live only 7.8 and 14 years, respectively (Frederickson, M. E. 2005). It is possible that \textit{A. octoarticulatus} colonies help \textit{C. nodosa} trees survive and grow until they are colonized by \textit{Azteca} spp. and can reproduce.

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\section*{Literature Cited}


Ant-Plant Conflict over Reproduction


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Left, Allomerus octoarticulatus workers patrol the young leaves of Cordia nodosa and protect them against insect herbivores. Top right, workers of this ant species also destroy C. nodosa flowers and floral buds by gnawing on the delicate tissues of the inflorescence. Bottom right, an undamaged C. nodosa inflorescence, for comparison. Photographs by Megan Frederickson.