



A castration parasite of an ant–plant mutualism

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Exploring the factors governing the maintenance and breakdown of cooperation between mutualists is an intriguing and enduring problem for evolutionary ecology, and symbioses between ants and plants can provide useful experimental models for such studies. Hundreds of tropical plant species have evolved structures to house and feed ants, and these ant–plant symbioses have long been considered classic examples of mutualism. Here, we report that the primary ant symbiont, *Allomerus* cf. *demerarae*, of the most abundant ant–plant found in south-east Peru, *Cordia nodosa* Lam., castrates its host plant. *Allomerus* workers protect new leaves and their associated domatia from herbivory, but destroy flowers, reducing fruit production to zero in most host plants. Castrated plants occupied by *Allomerus* provide more domatia for their associated ants than plants occupied by three species of *Azteca* ants that do not castrate their hosts. *Allomerus* colonies in larger plants have higher fecundity. As a consequence, *Allomerus* appears to benefit from its castration behaviour, to the detriment of *C. nodosa*. The *C. nodosa*–ant system exhibits none of the retaliatory or filtering mechanisms shown to stabilize cheating in other cooperative systems, and appears to persist because some of the plants, albeit a small minority, are inhabited by the three species of truly mutualistic *Azteca* ants.

Keywords: castration parasite; ant–plant; myrmecophyte; mutualism; eusocial evolution; cost of reproduction

1. INTRODUCTION

Since Janzen's (1966) seminal paper demonstrating the mutual benefits of association between *Pseudomyrmex* ants and bull's horn acacias, ant–plant symbioses have been considered prime examples of mutualism and cooperation (Huxley & Cutler 1991; Davidson & McKey 1993). A number of ant–plant mutualisms across a wide taxonomic range have now been verified experimentally (e.g. Janzen 1971; Letourneau 1983; McKey 1984; Huxley 1978; Schupp 1986; Fiala *et al.* 1989; Vasconcelos 1991; Yu 1994; Clarke & Kitching 1995; Treseder *et al.* 1995). Much less attention, however, has been paid to parasitisms of, or breakdowns in, ant–plant cooperation (Janzen 1975; McKey 1984; Young *et al.* 1997), despite widespread theoretical and empirical interest in cheating and parasitisms in the context of mutualisms (Trivers 1971; Axelrod & Hamilton 1981; Thompson 1982; Soberon M. & Martinez del Rio 1985; Bull & Rice 1991; Pellmyr & Huth 1994; Connor 1995).

Here we describe an intricate parasitism of an ant–plant mutualism, one likely to have resulted from a breakdown in cooperation between an ant–plant and one of its ant associates. We take advantage of the fact that both ant and plant are sessile and experimentally tractable to carry the measurement of costs and benefits to the level of fruit and ant alate (reproductive) production.

The ant–plant *Cordia nodosa* Lam. (Boraginaceae) is the most abundant ant–plant in south-east Amazonian Peru

(ca. 80–150 plants ha⁻¹ in lowland forest), hosting four ant species at Cocha Cashu Biological Station in Manu National Park (Department of Madre de Dios, south-eastern Peru). *C. nodosa* plants are understory treelets, most under 2 m tall. In this study, colonies of *Allomerus* cf. *demerarae* (Myrmicinae) inhabited 77.8% of the plants, three (currently undescribed) species of *Azteca* (Dolichoderinae) inhabited a total of 10.6%, and *Myrmelachista* spp. (Formicinae) inhabited 1.7% ($n_{\text{tot}}=1024$). The remaining 9.9% were not yet colonized or were partially inhabited by a variety of opportunistic 'tramp' ants. The *Allomerus* and *Azteca* species appear to be specialized symbionts of *C. nodosa*, since none has been collected from either any other ant–plant or elsewhere in the Madre de Dios region of Peru.

As in other ant–plant systems (Yu & Davidson 1997), the species of resident ant colony is determined at the sapling stage, when multiple queens colonize uninhabited saplings. Ants are housed in specialized stem swellings, called domatia (figure 1a), formed by the growth of an axillary bud back into the branch (Bailey 1924). Six leaves are produced with each domatium (=1 shoot). Thus, the number of domatia provides an index of both plant and ant colony size, and (as will be shown) serves as a common currency of interchange between ant and plant. This study was carried out at Cocha Cashu Biological Station in Manu National Park between 1991 and 1996, with the exception of some of the experimental invasions (see §2(b)(ii) below), which were undertaken at the Tambopata Jungle Lodge, also in Madre de Dios.

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2. METHODS

(a) *Measurements of plant and ant reproduction*

(i) *Fruit, flower and new shoot census*

In order to compare fruit production and plant growth across ant classes, 1024 *C. nodosa* plants were mapped along the trail system of Cocha Cashu Biological Station, and scored at the first census for ant inhabitants, light regime (treefall gap versus forest understorey), flower, fruit and new shoot production, and domatia number. Gaps were defined as the area of disturbed vegetation within and immediately bordering a treefall. Plants inhabited by different ant species were interspersed throughout the trail system. All plants were scored monthly for flower, fruit and new shoot production from the time they were first mapped in September–October 1994 until August 1995 (except December, which was omitted for logistical reasons). Plant growth was estimated by scoring domatia number again at the last census. To eliminate double counting from one month to the next, only green fruits were counted in the analysis of fruit production. Fruit were also scored by location on the plant: domatia, trunk apex and trunk. Ant vouchers for all censused plants have been deposited in the Museum of Comparative Zoology, Harvard University.

(ii) *Allomerus colony fecundity*

In order to assess the relationship between plant size and ant colony fecundity, the ant alates in 34 non-census population *Allomerus*-inhabited plants of varying sizes were collected in August 1995 along a transect. Each tree was scored for the number of domatia and numbers and sex of alates (ant reproductives).

(b) *Behavioural observations*

Three further experiments were conducted to (1) characterize the relationship between *Allomerus* and *C. nodosa* at the vegetative level, (2) to assess the probability of replacement of established *Allomerus* colonies by *Azteca* colonies, and (3) to contrast the foraging patterns of the two ant genera.

(i) *Protection from herbivory*

Eleven *Allomerus*-inhabited plants which were simultaneously producing two new shoots were chosen for experimentation. Within each plant, one shoot was assigned randomly as a control. On the other shoot, worker ants were excluded using a combination of TangleTrap™ (The Tanglefoot Co., MI, USA) and wire screening. After shoots had fully expanded, each pair was removed, and the total leaf area minus that lost to herbivory was measured using a Li-Cor™ (LI-COR Environmental Division, NE, USA) leaf area meter. Differences in leaf area were compared using a paired *t*-test.

(ii) *Experimental invasion*

Twenty-five plants inhabited by *Allomerus* and located less than 2 m from an *Azteca*-inhabited plant were identified. Each *Allomerus*–*Azteca* plant pair was connected using both twine and long palm leaf rachises. Plant pairs were monitored for three months.

(iii) *Ground baiting*

Baits of dried meat or cheese were placed 1 m from the base of 20 trees inhabited by *Allomerus* and 11 trees inhabited by *Azteca*. Baits were watched until retrieved by the resident ants, by non-resident foraging ants in the vicinity, or until 12 h had passed. As

a control, baits were placed directly on leaves of both *Allomerus*- and *Azteca*-inhabited host plants.

(c) *Statistical analysis*

Specific tests of comparison are cited in §3. 586 plants were analysed in the comparison of fruit production and net growth across ant class (537 *Allomerus*, 49 *Azteca*). Omitted from this analysis were (i) plants lacking either an *Azteca* or *Allomerus* colony, (ii) double-colony plants (see §3(a)), (iii) plants with incipient ant colonies not inhabiting the entire plant, (iv) plants which senesced, suffered a tree or branchfall, death or change of the resident ant colony during the census period (often due to predation by *Crematogaster* ants), or attack by *Trachysomus* sp. beetles (see §3(a)), and (v) plants in treefall gaps. Plants in treefall gaps ($n=166$), which have higher net growth, were analysed separately because *Allomerus*-inhabited plants were significantly underrepresented in gaps due to *Trachysomus* sp. attacks (see §3(a)). Since the main differences among ant species were between genera, results for the three species of *Azteca* were pooled for between-ant comparisons.

3. RESULTS

(a) *Behavioural observations*

Typically, colonization by one ant species precludes subsequent colonization on the same plant. Within the one-year census period, only 4 of 794 free-standing *Allomerus* colonies were replaced by an *Azteca* colony, and in these cases, plants hosting the colonies were either touching ($n=2$), or located within 1 m of each other ($n=2$). Experimental attachment of *Azteca*-inhabited to *Allomerus*-inhabited plants ($n=25$) failed to produce invasions in all cases.

Both *Azteca* and *Allomerus* ants vigorously patrolled new shoots, and attacked and ate insect prey. The experimental removal of *Allomerus* ants from new shoots resulted in a significantly higher loss of leaf area to herbivory compared with within-plant controls ($n=11$; mean leaf area, without ants = 74.2 cm² (s.d. 75.2), with ants = 158.5 cm² (s.d. 109.9); paired *t*-test, $t=2.425$, d.f. = 10, $p=0.036$).

Plants occupied by *Allomerus* experienced differential herbivory by a cerambycid beetle. The beetle, *Trachysomus* sp., selectively girdles and kills trunks of large *Allomerus*-inhabited *C. nodosa* trees, thereby providing a source of dead wood for its larvae. *Trachysomus* beetles probably concentrate their attacks on *Allomerus*-inhabited plants rather than on *Azteca*-inhabited plants because, in the former, workers do not patrol the trunk, whereas *Azteca* workers constantly move between their host and satellite carton nests located on neighbouring vegetation. For example, in the ground baiting experiment, none of the 20 baits placed near *Allomerus*-inhabited plants was found by *Allomerus* workers, even after 12 h. In contrast, when baits were placed on host plants, they were readily consumed by *Allomerus* workers. Seven of 11 baits placed near the four *Azteca*-inhabited plants were found by *Azteca* workers within 5 h, and of the seven, five were found within 90 min (Monte-Carlo contingency table test (Engels 1988), $p=0.0002 \pm 0.0001$ s.e.).

During the census period, *Trachysomus* beetles girdled 29 *C. nodosa* trees: two without ants and 27 with *Allomerus*. The

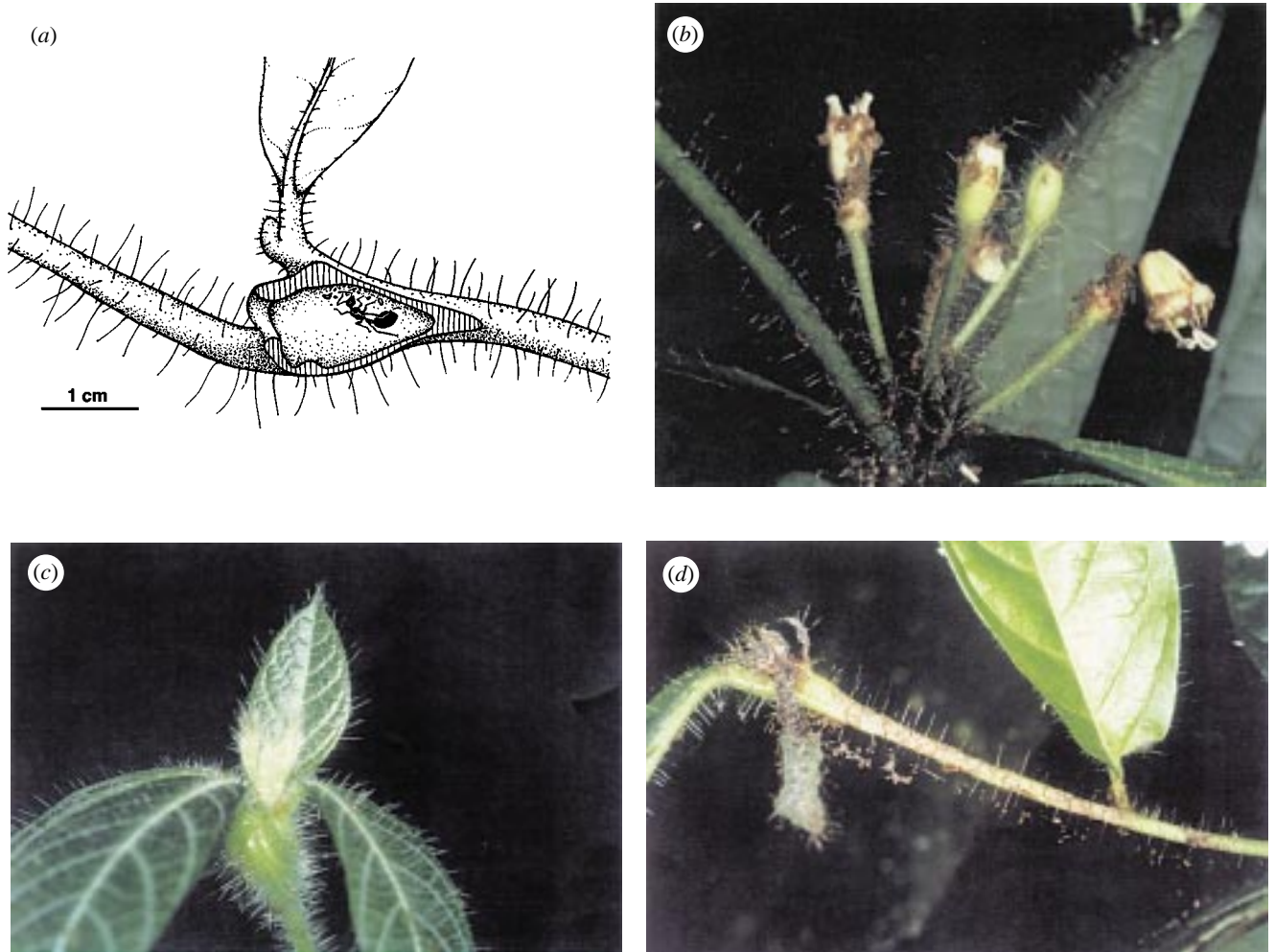


Figure 1. (a) Schematic drawing of a *C. nodosa* branch with leaves and domatium, and a colonizing *Allomerus* queen with brood. (b) *Allomerus* workers attacking and destroying the flowers of their host plant. Usually, workers attack flowers at the bud stage, and so castration is not obvious to the casual observer. (c) Almost fully developed floral buds on a young shoot containing one domatium and six new leaves. (d) Young shoot (originally with floral buds) dead from *Allomerus* worker attack. Note the necrotic spots where worker ants chewed through plant tissue.

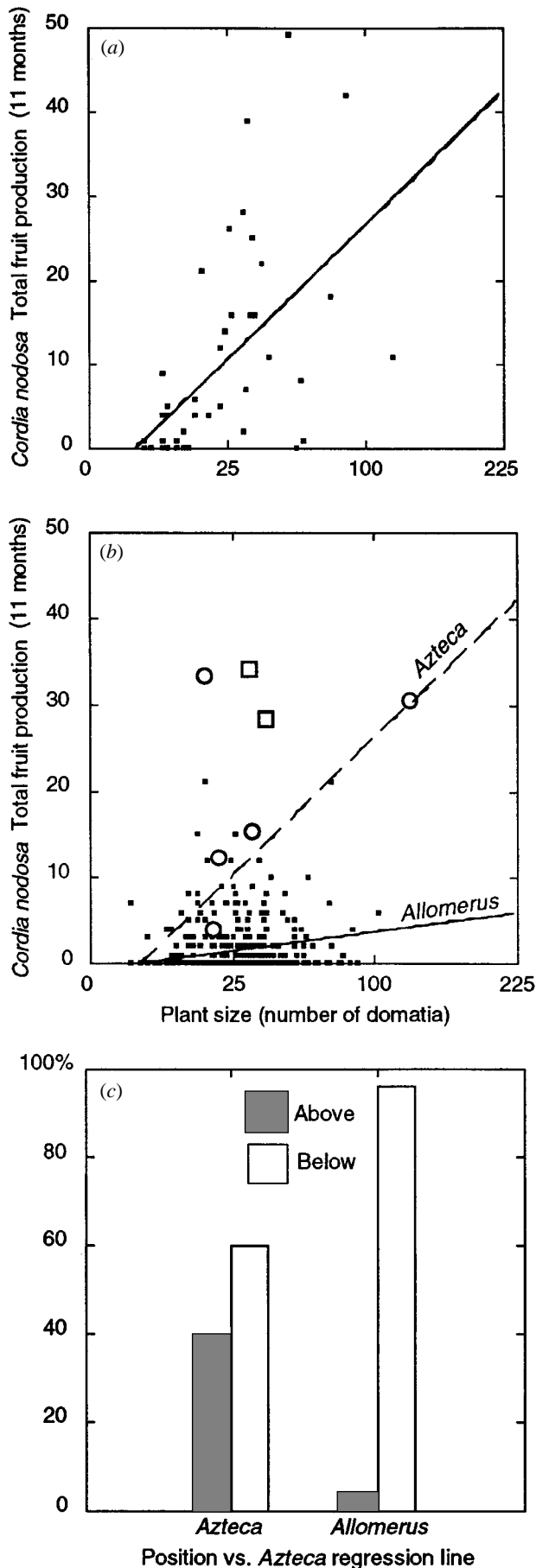
beetles preferred large plants with sufficiently thick trunks (> 2 cm) for larval feeding: the average tree of *C. nodosa* attacked by beetles contained 46 domatia, whereas the average tree inhabited by *Allomerus* contained 26 domatia (Mann–Whitney $U=3877.5$, d.f.=1, $p < 0.001$). Attacks were concentrated in or near gaps (22 of 29 attacks, contingency table test, $G=27.60$, d.f.=1, $p < 0.001$), and may explain why *Allomerus*-inhabited plants are rarely found in gaps, as opposed to *Azteca*-inhabited plants (*Allomerus*: 16.4% in gaps, versus *Azteca*: 33.0%, $G=15.419$, d.f.=1, $p < 0.001$). Interestingly, ant queens of both genera colonized saplings without regard to light regime (D. Yu, unpublished data). Girdled *C. nodosa* plants usually lost all above-ground biomass, and resident colonies were either much reduced (if plants were able to resprout from the trunk base), or killed outright.

Allomerus worker ants attack and destroy the floral buds and flowers of their host plant (figure 1b). This attacking behaviour contrasts strongly with the leaf protection behaviour exhibited by the same workers. Typically, floral buds are ignored by workers until the buds are close to full size. Individual ants then start to antennate buds

vigorously. As more ants recruit to the buds, workers concentrate their attacks at the pedicel, although individual ants will also attack and penetrate the calyx. Within 24 h, the pedicels have usually been cut through to the point that the buds then desiccate. In the rarer cases when the floral buds are able to open before being destroyed (e.g. figure 1b), the ants have been observed to attack petals, styles and stamens as well as the pedicels.

Colonies vary as to when attacks are initiated. Most colonies were observed attacking floral buds just before anthesis, some colonies attacked floral buds much earlier in development, and still others allowed at least some buds to open before attack. In the latter cases, it is possible that some of the flowers donated pollen before the attack was complete, and some of these flowers also successfully set fruit (figure 2b). Finally, in a small number ($n=7$, $< 1\%$) of *Allomerus*-inhabited plants in the sample, workers ignored flowers, and the plants fruited normally (figure 2b).

The ants do not appear to be ingesting any of the material removed from the buds or flowers. Most tissue simply desiccates and remains in place until it drops. Any removed tissue may be deposited in the carton which



overlies trails along the branches and trunk of the host plant. These trail 'roofs' consist primarily of ant frass, insect prey remains, dead ants and dirt, and serve a defensive function by allowing workers to attack invading ants from below (D. Yu, personal observation). Thus, the ants do not seem to be gaining any substantial direct benefit from the buds or flowers.

The contrast between leaf-protecting and flower-destroying behaviours is most obvious in the cases when floral buds are found on new shoots (figure 1c). Worker ants ignore developing floral buds even while patrolling and protecting the shoot against herbivory. Only when leaves are almost fully developed do workers turn to attacking floral buds. Not all floral buds are successfully attacked before the flowers open, apparently due to the delay before attacking. In one instance, workers were observed to attack the entire shoot, destroying not only the floral buds but also the developing leaves and domatium (figure 1d).

Removal of flowers reduces fruit production dramatically (figure 2): more than 70% of the *Allomerus*-inhabited plants studied over the 11-month census period produced no fruit. *C. nodosa* does not reproduce vegetatively. Within the census period, 53% of the fruit production in the *C. nodosa* population came from the small population of *Azteca*-inhabited plants; extrapolation suggests that *Allomerus* reduces the total fruit production in the *C. nodosa* population by about 80%. Omitting gap plants in this analysis (see §2(c)) is conservative because, in gaps, fruit production is significantly higher in *Azteca*-inhabited but not in *Allomerus*-inhabited plants (D. Yu, unpublished data). In addition, 12 plants were found that hosted both *Allomerus* and *Azteca* colonies in different branches of bifurcating trunks (double-colony plants). In these, the *Azteca*-inhabited portion flowered and fruited normally, whereas the *Allomerus*-inhabited portion did not.

Figure 2. Scatterplots of total fruit produced over the 11-month census period against plant size (domatia number, square root scale). Because data were not normally distributed, we constructed a nonparametric test. Linear regressions were run through both data sets, dividing each data set into above-the-line and below-the-line portions. If the fruit production-to-plant size relationship is not significantly different across ant classes, then a linear regression from one data set should divide the other data set into above- and below-the-line portions approximately equal to the proportions in the first data set (null hypothesis). A contingency table test can then be used to assess significant departures from the null hypothesis. (a) The relationship between plant size and fruit production for *Azteca*-inhabited plants ($n=49$). (b) The same relationship for *Allomerus*-inhabited plants ($n=537$). The regression line from (a) (dashed line) is presented in (b) for comparison. Circles denote plants in which workers were observed not to castrate flowers. Only five of seven such plants are shown because one plant died in a treefall, and the other was located in a gap (see §2(c)). Squares denote two plants with greater than 50% of fruits produced on the trunk or trunk apex (see also figure 5). High production of fruits in these seven plants support the interpretation that it is the destruction of flowers that reduces fruit production and not that *Allomerus*-inhabited plants are inherently producing less fruit. (c) Contingency table test. Significantly more *Allomerus*-inhabited plants fell below the *Azteca* regression line than did *Azteca*-inhabited plants ($G=45.306$, d.f. = 1, $p < 0.001$).

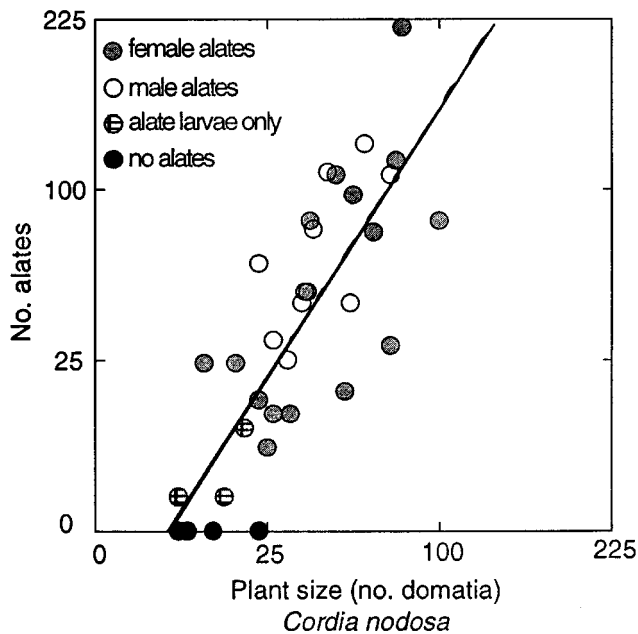


Figure 3. Linear regression of the standing count of *Allomerus* alates (ant reproductives) against plant size (square-root scale). Domatia number was positively related to the total number of larval, pupal and adult reproductives in the colony (reproductives^{1/2} = $-3.32 + 1.57 \times \text{domatia}^{1/2}$, $n = 34$, $p < 0.001$, $R^2 = 0.670$). The same regression, using alate dry weight, explained less of the variance ($n = 26$, $R^2 = 0.432$, $p = 0.001$). Colony sex ratios were strongly bimodally distributed, with all but four colonies producing only one sex, and those four producing primarily one sex or the other.

(b) Plant and ant reproduction

Preventing fruit production would benefit the resident ant colony if plant resources were reallocated to domatia and if fitness of the ant colony was higher in larger plants. Both of these conditions appear to be met. (1) Per cent net gain in plant size was significantly higher in *Allomerus*-inhabited plants (*Allomerus*: 29.7%, *Azteca*: 11.7%, Mann-Whitney $U = 10\ 035.0$, d.f. = 1, $p = 0.011$). Starting plant size was not significantly different across ant inhabitants (*Allomerus*: 25.5 domatia, *Azteca*: 26.4 domatia, Mann-Whitney $U = 12\ 022.0$, d.f. = 1, $p = 0.32$). (2) Production of ant alates (reproductives) varied positively with domatia number (figure 3), suggesting that nest size limits ant fecundity in this system. Lower net growth in *Azteca*-inhabited plants was due to a higher rate of senescence of leaves and domatia; rates of new shoot production did not differ between ant classes (ANCOVA, domatia number^{1/2} as the covariate, d.f. = 1, $F = 0.818$, $p = 0.366$).

The difference in net growth between fruiting, *Azteca*-inhabited plants and non-fruiting, *Allomerus*-inhabited plants is significant only for plants in the forest understorey. This is because plants in and near gaps ($n = 166$) have a higher rate of net growth than plants in the understorey (most likely due to increased carbon availability in the former group). However, *C. nodosa* in and next to gaps are also disproportionately inhabited by *Azteca* because of the gap-centred attack of *Allomerus*-inhabited *C. nodosa* by *Trachysomus* sp. beetles (see §3(a) above).

A substantial proportion of the fruit in *C. nodosa* plants is found on the trunk, trunk apex, and rarely, on unswollen

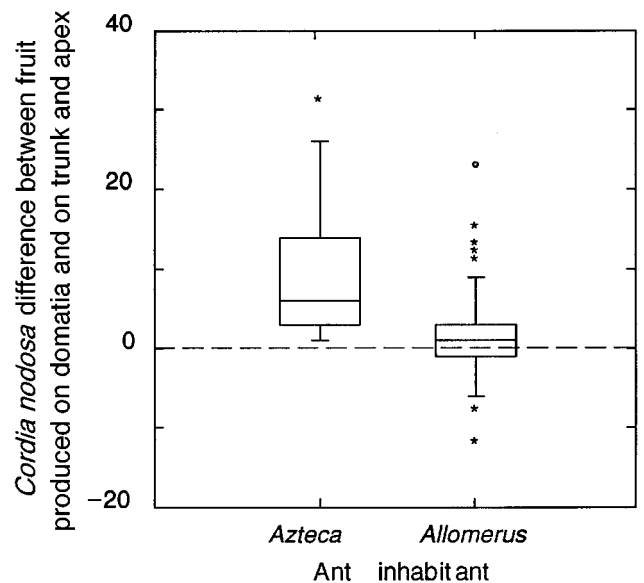


Figure 4. Box and whisker plot of the spatial distribution of fruit production on *Allomerus*- and *Azteca*-inhabited plants. Within each fruit-producing plant, the number of fruit produced on the trunk or apex was subtracted from the number produced on the domatia. Centre line denotes median value, the box encloses the inner two quartiles (midrange), and the lines encompass a further 1.5 times the mid-range (Wilkinson *et al.* 1992).

branch nodes which lack domatia. These sites are usually free of patrolling ants. Of the 148 *Allomerus*-inhabited plants producing any fruit over the course of the census period, 27% produced more fruit on the trunk or trunk apex than on the domatia, indicated by values less than zero (figure 4, see also figure 2b). In contrast, none of the 31 *Azteca*-inhabited plants producing fruit over the course of the census produced more fruit on the trunk or apex than on the domatia ($G = 17.47$, d.f. = 1, $p < 0.001$).

4. DISCUSSION

Because *Allomerus* drastically reduces the expected fitness of its host plant by preventing association with *Azteca*, we classify *Allomerus* as a castration parasite of the *C. nodosa*-*Azteca* mutualism. We use the term 'castration' here, with reference to earlier scientific literature, to mean the physical destruction of either male or female reproductive organs (Malm 1881; Baudoin 1975; Clay 1991). We further refer to *Allomerus* as a 'parasite' because there exists an alternative and more beneficial symbiont, *Azteca*. That is, association with *Allomerus* imposes an opportunity cost on its host plant. Parasites of mutualisms often impose opportunity rather than direct costs (Yu 1997). For example, nectar-robbing hummingbirds may occasionally effect pollen transfer, but are still considered pollination parasites because removal of nectar dissuades more effective pollinators from visiting (McDade & Kinsman 1980).

In earlier work, Young *et al.* (1997) report that the ant *Crematogaster nigriceps* destroys the axillary shoots of the swollen-thorn acacia, *A. drepanolobium*. Although they do not identify the ant as a castration parasite, they note

that inflorescences are primarily found on axillary shoots, that pruning of such shoots prevents most flowering and fruiting, and that pruned plants have more extra-floral nectaries and appear to have healthier leaves. However, this study did not address the reproductive consequences for the ant of its pruning behaviour.

Azteca-inhabited plants may also be the primary source of pollen for plants inhabited by either ant genus. Pollen production by *Azteca*-inhabited plants is probably important to the persistence of the population since *C. nodosa* is distylous (Miller 1985), which can indicate obligate outcrossing. Experimental exclusion of *Allomerus* workers from floral buds led to normal flower development, but fruit developed in only 1 out of 95 flowers, the rest being aborted ($n=17$ plants) (D. Yu, unpublished data). Abortion of so many flowers in plants not otherwise producing fruit leads us to expect pollen limitation to be more important than resource limitation in causing floral abortion, although this needs to be examined experimentally.

The correlation between the prevention of fruiting in host plants and an increase in the net rate of domatia production suggests that castration is an adaptation of *Allomerus* to increase colony fecundity. This interpretation is supported by experimental results from plant physiological studies showing that reproduction exacts a cost in plants (reviewed in Bazzaz & Ackerly 1992). In fact, the observed higher rate of senescence of old shoots of *C. nodosa* inhabited by *Azteca* is consistent with experimental studies showing that nutrient stress or fruiting can increase the rate of leaf senescence in other plant species (Sinclair & De Wit 1975; Wada *et al.* 1993; Pons & Pearcy 1994). Shoot (domatia) senescence in *C. nodosa* may be mediated by translocation of nutrients (especially nitrogen) to the developing fruits. In addition to increased net plant growth, *Allomerus* workers could also benefit if the lack of fruiting increased nutrient availability in plant sap, which workers harvest indirectly by tending pseudococcids in domatia walls.

An increase in domatia number benefits *Allomerus* colonies because the number of domatia appears to regulate the rate of ant alate production, simply by limiting space. Most domatia are not large enough to house more than three or four alates (e.g. figure 1a). In contrast, *Azteca* colonies do not appear to be limited by host-plant size since *Azteca* colonies regularly construct satellite carton nests on neighbouring vegetation and on the host plant itself. We hypothesize that host-plant size limitation has been one of the selective factors favouring the evolution of castrating behaviour in *Allomerus*.

An alternative explanation for the correlation between reduced fruiting and increased growth is that *Allomerus* colonies may be choosing in some way to inhabit inherently faster-growing plants. In order for *Allomerus* to 'choose' in some way to inhabit faster-growing plants, queens would have to be able to assess future plant growth when colonizing saplings. It seems unlikely that queens have a choice of saplings. Because of high dispersal mortality and intense competition, queens appear to try to colonize the first sapling they land on, rather than risking another trip in search of a (possibly) faster-growing plant. Although colonization of new saplings was observed on only a few occasions during this study, queens immediately colonized unoccupied domatia and shed their wings

accordingly. Moreover, in a tropical forest understorey, light is a limiting resource, and its availability is extremely variable over even short time periods (Chazdon & Pearcy 1991), thereby rendering correct long-term prediction unlikely.

The *C. nodosa*–*Allomerus* interaction presents a striking example of cheating in a mutualism, and poses the difficult task of identifying factors that keep cheating from driving the mutualism to extinction. In the case of fungus-growing leafcutter ants, such as *Atta cephalotes*, workers destroy the hymenial tissue in the developing basidiomata of their developing fungus (Fisher *et al.* 1994). Stability is maintained in these systems because the fungus can be propagated vegetatively by their ant hosts, who pass the fungus from one generation to the next by vertical transmission (Axelrod & Hamilton 1981; Clay 1991; Chapela *et al.* 1994). However, for cases where both partners in a mutualism disperse separately and reproduction requires sex, other mechanisms for persistence are necessary.

Cooperation in ant-plants can be stabilized against cheating if the host plant can retaliate against cheaters, filter out potential cheaters before investment, derive by-product benefits from selfish behaviour of the other partner and/or parcel out rewards in return for bouts of cooperative behaviour (Trivers 1971; Axelrod & Hamilton 1981; Bull & Rice 1991; Risch & Rickson 1981; Keller & Ross 1993; Pellmyr & Huth 1994; Connor 1995). None of these mechanisms is immediately apparent as the primary agent stabilizing the system. Retaliation in the context of the *C. nodosa*–*Allomerus* parasitism would require that the host plant somehow eliminate the colony or reduce the colony's fitness upon castration, neither of which occurs. Nor do saplings of *C. nodosa* appear to filter out colonizing *Allomerus* queens. At Cocha Cashu, colonizing *Allomerus* queens are twice as abundant as *Azteca* queens in naturally occurring saplings, and the former suffer a lower rate of mortality during colony establishment (Yu & Pierce 1998).

However, several factors could play contributing roles in stabilizing the *C. nodosa*–ant mutualism. By attacking only *Allomerus*-inhabited plants, the beetle *Trachysomus* sp. is effectively acting as a keystone predator (Paine 1966), reducing the production of *Allomerus* alates. In addition, a substantial proportion of fruits in *Allomerus*-inhabited plants are found on the trunk, trunk apex, and rarely, on unswollen branch nodes which lack domatia (figure 4), all sites where patrolling ants are rare. Selection by the ants may have resulted in these unusual fruiting locations. Also interesting is the production of floral buds on immature shoots, some of which successfully bear fruit (figure 1c). The simultaneous production of flowers and leaves on a developing shoot is, to our knowledge, unreported in the literature and suggests a change in plant developmental patterns in response to castration behaviours. Finally, the observed variation across colonies in rates of attacking behaviour may be key in understanding why many *Allomerus*-inhabited plants are able to produce successfully at least some fruit (figure 2b), albeit at a low rate. Especially intriguing are the small number of *Allomerus*-inhabited plants where workers were observed to ignore flowers and thus allow the plants to fruit normally (figure 2b). How these plants differ from conspecifics is unknown; possible explanations relating to plant size or light regime

have been ruled out (D. Yu, unpublished results), and the workers from non-castrating colonies are morphologically indistinguishable from castrating workers.

Variation in attack rates is likely to be caused by variation in the ability of resident ants to differentiate between vegetative and reproductive structures. Indeed, the main trait enabling *Allomerus* to develop castrating behaviour is the ability to identify reproductive structures. The cues used in distinguishing flowers from other plant parts may shed light on the evolutionary origins of the castrating behaviour. A comparative life history analysis of congeneric species of *Allomerus*, all of which inhabit ant-plants, and of *C. nodosa* and its close relatives, may illuminate conditions that predispose interactions to the kind of parasitism exhibited by the *Cordia*–*Allomerus* system.

The persistence of *Azteca*, despite its local rarity, appears to play the central role in maintaining the *C. nodosa* population and thus the *C. nodosa*–ant mutualism. That the *C. nodosa*–ant system is stable is suggested not only by its local abundance but also by the extensive geographic range of the system. *Azteca* and (castrating) *Allomerus* have been found coexisting in *C. nodosa* across multiple sites in Madre de Dios, Peru and as far away as Jatun Sacha Biological Station in Ecuador (D. Yu, unpublished results). Wheeler (1942) also reported observing coexisting *Allomerus* and *Azteca* in *C. nodosa* in Guyana.

We show elsewhere (Yu & Pierce 1998; Yu & Quicke 1997) that *Azteca* and *Allomerus* appear to coexist via a competition–colonization trade-off on the single, limiting resource represented by their host plants. *Azteca* queens are better colonizers because they arrive at saplings at a rate four times higher than *Allomerus* queens. *Allomerus* queens are better competitors because they have higher brood production rates. As predicted by the ‘habitat destruction hypothesis’, which can be used as a test of whether species are coexisting by means of a competition–colonization trade-off (Nee & May 1992), the relative abundance of *Azteca* colonies rises from 10% in sites with high plant density (100 plants ha⁻¹) to 60% in sites with low plant density (10 plants ha⁻¹) (Yu & Pierce 1998).

The *C. nodosa*–ant system is an extreme example of a class of mutualisms (Janzen 1975; McKey 1984; Letourneau 1990; West & Herre 1994; Pellmyr *et al.* 1996; Young *et al.* 1997), in which both parasitic and mutualistic species compete for the resources of a host species (type II *aprovechados* (cheaters): Soberon M. & Martinez del Rio 1985), and in which mechanisms stabilizing cheating are apparently absent or weak (Yu 1997). In all these systems, the long-term persistence of mutualistic relationships poses a challenge to evolutionary and ecological theory, and we suggest that species coexistence mechanisms, such as the one identified for the *C. nodosa*–ant symbiosis, may be commonly responsible for preventing parasitic species from driving interspecific mutualisms extinct.

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