

international monitoring to assess the success of acidic deposition control measures. □

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**Sterilization and canopy modification of a swollen thorn acacia tree by a plant-ant**

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Obligate symbioses between specialized arboreal ants and plants have evolved independently in many lineages<sup>1,2</sup>. Ant-plants (myrmecophytes) typically provide hollow nest cavities and nutrition to the occupying ant colony<sup>1,3–6</sup>. In turn, resident plant-ants often protect their hosts from herbivory<sup>7–11</sup> and/or overgrowth by surrounding vegetation<sup>12,13</sup>. As individual plants are rarely occupied by more than one ant colony<sup>14–17</sup>, co-occurring plant-ant species compete intensely for hosts<sup>13,14,18,19</sup>. In such multi-species systems, ecological interactions among potential partners may lead to the evolution of cheating<sup>20,21</sup>. Previous studies have revealed that some specialized plant-ants are effectively parasites of their host-plants<sup>8,18,22,23</sup>, but the selection pressures favouring such behaviours are poorly understood. Here we describe host parasitism in an east African plant-ant that prunes and sterilizes its host-tree canopies, apparently to minimize contact with competitively dominant ants occupying neighbouring trees. We propose that the high density of ant-trees and low diversity of tree species in this savanna habitat have selected for induced, parasitic pruning of host trees by this competitively subordinate ant species.

Whistling Thorn (*Acacia drepanolobium*) trees dominate vast areas of savanna on black cotton soils in upland east Africa<sup>24,25</sup>. At each branch node, *A. drepanolobium* trees produce either a pair of slender thorns or a swollen thorn pair joined by a bulbous, hollow base 1.5–6 cm in diameter (Fig. 1). When living on a tree, ants chew



**Figure 1** Close-up of *A. drepanolobium* branches showing axillary leaves, paired slender thorns and a node occupied by a fused swollen thorn pair. To show architectural features clearly, this photograph was taken at the beginning of the rainy season, when relatively few axillary leaves were persistent on older growth. Resident ants had not yet chewed entry holes into the recently formed swollen thorn (centre). Swollen thorns are produced even in the absence of ants<sup>26</sup>.

entry holes into the swollen thorn bases and use the hollow interiors to house workers and raise brood<sup>25,26</sup>. Four species of specialized plant-ants co-exist within most populations of *A. drepanolobium*<sup>26</sup>. In our study site at the Mpala Research Centre in Kenya (36° 50' E, 0° 15' N), *Crematogaster mimosae* occupies almost 50% of the trees, while the remaining trees are divided between three other ant species: *Crematogaster sjostedti*, *Crematogaster nigriceps*, and *Tetraponera penzigi*. Less than 1% of trees over 0.5 m tall are unoccupied. Three of these ant species occur only on *A. drepanolobium* trees within this ecosystem; *C. sjostedti* also occupies *Acacia seyal*, a far less abundant tree which can also produce swollen thorns<sup>25</sup>.

Canopy architecture varies significantly among *A. drepanolobium* trees occupied by the four ant species in our study site (Wilk's Lambda:  $P = 0.0179$ ,  $F = 3.174$ ; degrees of freedom (d.f.) = 15, 14). Trees occupied by *C. nigriceps* are characterized by an unusually high degree of branching, reduced apical dominance and lateral spread, large swollen thorns and high swollen thorn density (Fig. 2). There are two alternative hypotheses that could explain this pattern. *C. nigriceps* colonies may selectively occupy trees with this type of architecture; or *C. nigriceps* may modify the architecture of host-tree canopies to increase secondary branching at the expense of lateral canopy spread.

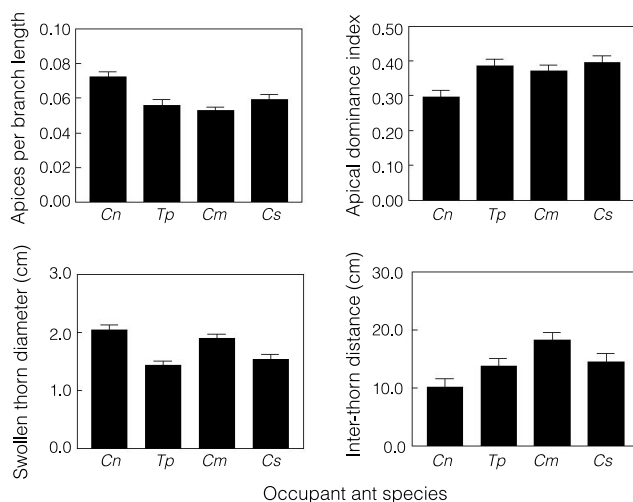
Field observations provide evidence for active canopy modification by *C. nigriceps*. *A. drepanolobium* trees produce dense 'cushions'<sup>24</sup> of axillary buds below each pair of stipular thorns. Cushions remain active for at least two years, producing leaves, branches and/or flowers during subsequent growth cycles. At our study site, trees occupied by *C. nigriceps* are uniquely characterized by the absence of most axillary cushions<sup>25</sup>. Undamaged cushions occur principally at nodes with swollen thorns, and it is from these nodes that most leaves and lateral branches arise. We observed that *C. nigriceps* workers aggregate on growing shoots of the host tree, where they rapidly destroy most axillary cushions and eventually kill the apical meristem. These pruning activities probably cause the unique canopy architecture associated with *C. nigriceps*. Moreover, pruning sterilizes the host-tree; destruction of cushions and occupancy by *C. nigriceps* are associated with greatly reduced flower production by *A. drepanolobium*<sup>25</sup>.

To test the hypothesis that *C. nigriceps* ants actively modify the branching architecture of their host trees, we assigned one-half of the trees used for architectural measurements to an ant-removal treatment, while the other half served as controls. Two swollen thorn nodes on recent growth were selected at random on each tree. The number of branches emerging from each node were counted before treatments in June 1996, and after two full growing seasons in December 1997.

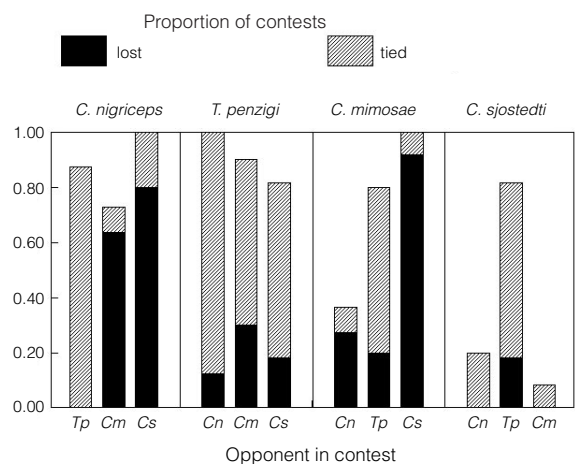
The ant-removal experiment confirmed that *C. nigriceps* significantly increase branching in canopies of their host trees. On control trees continuously occupied by *C. nigriceps*, branch production at swollen thorn nodes increased over 40% from 1996 to 1997. In contrast, on trees from which *C. nigriceps* had been removed, the numbers of branches per node decreased 25% over the same interval. These treatment-dependent changes in architecture were virtually absent on trees occupied by *C. sjostedti*, *C. mimosae* or *T. penzigi*. Most axillary bud cushions were destroyed on the post-1996 growth of control trees occupied continuously by *C. nigriceps*, but not on other trees. None of these trees flowered during the course of the experiment.

Competition for host trees leads to violent conflicts between the four species of acacia ant occupying *A. drepanolobium*. At our study site, we have observed a number of take-over raids in which ants from nearby *C. mimosae* or *C. sjostedti* colonies stream onto trees occupied by either *C. nigriceps* or *T. penzigi* and attempt to dislodge workers and brood from inside the swollen thorns. Field experiments confirmed that the four ant species vary markedly in their ability to take over trees forcefully and to defend their trees against take-overs. We staged conflicts between colonies of different species by tying together branches of two adjacent trees, each occupied by a different ant species. *C. nigriceps* was evicted from its host tree more than any other ant, losing 80% of the time in conflicts against *C. sjostedti* and 64% of the time against *C. mimosae* (Fig. 3). In contrast, although *T. penzigi* was rarely the aggressor, it successfully defended its host tree from attack 71% of the time. These experiments show that *C. nigriceps* colonies are unusually vulnerable to take-over when their host trees come into contact with colonies of the competitively dominant ants *C. sjostedti* and *C. mimosae*.

As trees grow taller and their canopies spread laterally, contacts



**Figure 2** Canopy attributes of *A. drepanolobium* trees occupied by four different species of acacia ants. Ant species: Cn, *C. nigriceps*; Tp, *T. penzigi*; Cm, *C. mimosae*; Cs, *C. sjostedti*. For five architectural measurements, multivariate analysis of variance showed that canopy architecture varies significantly among occupant ant species; least-squares means and standard errors shown are based on that analysis. In this study, the length of slender thorns did not vary significantly among species of ant occupants and so is not shown.



**Figure 3** Outcomes of staged conflicts between colonies of different ant species inhabiting neighbouring *A. drepanolobium* trees. There were 8–12 encounters between each pair of ant species. The species listed across the top of the Figure was the loser if it was displaced by the opposing colony from most or all of its joined host tree. A tie was scored if both colonies retained their host trees during six months following joining. Species of opposing colonies (below x axis): Cn, *C. nigriceps*; Tp, *T. penzigi*; Cm, *C. mimosae*; Cs, *C. sjostedti*.

with neighbouring tree canopies and potentially hostile ant colonies become more likely. In a random survey of 1,796 trees throughout the study site, we found that the probability of canopy contact with adjacent trees increases from 6.3% in trees less than 1.0 m to 34.0% in trees more than 3 m in height. Tall trees are predominately occupied by *C. sjostedti* and *C. mimosae*<sup>25</sup>, so the lateral canopy spread associated with tree growth presents a significant danger to competitively subordinate colonies of *C. nigriceps*.

As trees occupied by *C. nigriceps* grow, they show significantly less lateral canopy spread than trees occupied by the other three ant species. Analysis of covariance showed that canopy spread increases significantly with height ( $P < 0.0001$ ;  $F = 378.75$ , d.f. = 1,294), and varies significantly among ant occupants ( $P = 0.0056$ ;  $F = 4.29$ , d.f. = 3,294), with *C. nigriceps* trees showing the least lateral spread. The significant interaction between height and ant occupant ( $P < 0.0001$ ;  $F = 11.28$ ; d.f. = 3,294) revealed that the increase in lateral spread with height in trees occupied by *C. nigriceps* (0.296) is roughly half that for trees occupied by other ants (0.532–0.72). Quadratic regressions showed that trees occupied by *C. nigriceps* have diminishing rates of lateral canopy growth with increasing height, whereas canopy spread and height are linearly related in trees occupied by the other ant species. Together, these observations and experiments indicate that canopy pruning by *C. nigriceps* colonies may reduce potential contacts between their host trees and ant colonies on neighbouring trees.

In the *A. drepanolobium* system, detection of neighbouring ant colonies should be possible because at least three of the ant species produce potent alarm pheromones when distributed<sup>26,27</sup>. Moreover, because shoot pruning is time consuming for the resident ant colony and severely detrimental to the host tree, one might expect pruning to be conditionally induced by the presence of potentially aggressive colonies nearby. To test this hypothesis, we surveyed a random sample of 555 trees to determine whether canopy geometry is affected by proximity to neighbouring trees and ant colonies. As predicted, canopies of *C. nigriceps* trees were highly asymmetrical, showing significantly less lateral spread in the direction of neighbouring trees occupied by different ant colonies, and tending to extend outwards into open space or towards nearby trees occupied by the same colony ( $P = 0.0047$ ; Fig. 4). In contrast, the canopy geometry of trees occupied by the other three ant species was independent of neighbouring trees and colonies ( $P > 0.45$  in all

cases). These measurements indicate that *C. nigriceps* may selectively prune their host trees to avoid canopy contact with neighbouring ant colonies.

We propose that the evolution of host-tree pruning and sterilization by *C. nigriceps* ants has been driven by three attributes of the black cotton savanna community: the high density of ant-acacia trees; low tree-species diversity; and the presence of competitively dominant plant-ants using the same host-tree species. Other studies have shown that competitively subordinate plant-ants prune surrounding vegetation away from their hosts, presumably to eliminate arboreal pathways by which dominant ants can attack<sup>19</sup>. Because this type of pruning behaviour also reduces the susceptibility of the host plant to fire and overgrowth<sup>12,28</sup>, it poses no threat to the plant-ant mutualism. In contrast, because the canopy in black cotton habitats is virtually a monoculture of *A. drepanolobium* trees, workers would certainly be attacked by aggressive, resident colonies if they attempted to prune the canopies of nearby trees. Instead, competitively subordinate colonies of *C. nigriceps* prune and consequently sterilize their own host tree to minimize the risk of contact with more dominant ants. Our study reinforces the view that there is a fine line between mutualism and parasitism<sup>20,21</sup>, and that the attributes of the ecological community as a whole may determine the direction in which any given ant-plant association evolves<sup>13</sup>. □

## Methods

### Analysis of architectural traits

For each of 242 trees 0.75–2.0-m tall along four 200-m transects, we measured the base diameters of swollen thorns, lengths of slender thorns and branch distances between recently produced swollen thorns at two randomly canopy locations. On two branch systems per tree, we counted apices per total branch length to estimate the amount of branching, and measured the tendency for new growth to spread laterally away from the main stem as the ratio of longest shoot length to summed secondary shoot lengths (the 'apical dominance index'). The General Linear Models procedure of SAS<sup>29</sup> was used to conduct a multivariate analysis of variance (ANOVA); the effect of ant species (a fixed factor) was tested over the ant species-by-transect interaction. The effects of transect and ant-by-transect interaction were not statistically significant ( $P > 0.30$ ).

### Ant-removal methods

For trees assigned to the ant-removal treatment, all swollen thorns were cut open. Ants were brushed from the canopy, and a barrier of Tanglefoot and Teflon tape was placed around the tree's stem to prevent recolonization. On control trees we cut off the pair of slender thorns nearest to each swollen thorn; ants were distributed but not removed.

### Statistical analysis of the effects of ant removal on branching

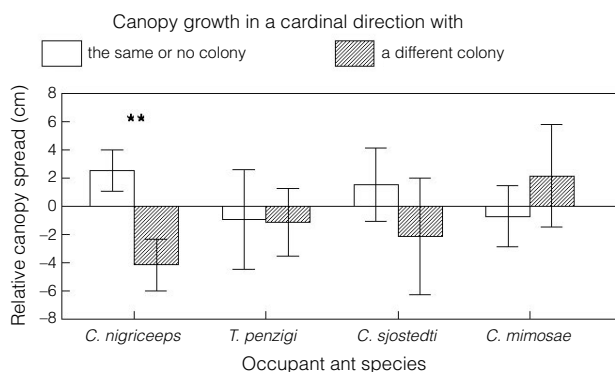
As there was no significant variation in branching between trees occupied by *T. penzigi*, *C. mimosae*, and *C. sjostedti*, these three species were pooled in a repeated-measures ANOVA<sup>29</sup>. Occupant ant species (*C. nigriceps* versus others) and treatment (ant removal versus control) were the between-subjects factors in the model; year was the within-subject factor. The number of branches per swollen thorn node was much greater in trees originally occupied by *C. nigriceps* than those occupied by the other three species ( $P < 0.0001$ ;  $F = 62.75$ ; d.f. = 1,151). The significant year-by-treatment interaction ( $P < 0.002$ ) showed that the ant-removal treatment increased branching over time, principally owing to trees occupied by *C. nigriceps*. In the overall ANOVA, there was a significant interaction between year, initial *C. nigriceps* occupancy and ant-removal treatment ( $P = 0.0104$ ;  $F = 6.729$ ; d.f. = 1,151). In a second ANOVA conducted just for the other three ant species, the interaction between year and removal treatment was not significant ( $P = 0.321$ ;  $F = 0.993$ ; d.f. = 2,110).

### Staging of inter-colony conflicts

In staging conflicts between neighbouring colonies of different species, we matched experimentally joined host trees by height and numbers of swollen thorns. Each pair of ant species was used in 8–12 trials. Colonies of the *Crematogaster* species often occupy multiple trees, and we did not prevent recruitment from other trees during the experiment. A tie was scored for each participating species when neither colony displaced the other from the majority of its joined tree over 6 months. Take-over of a joined tree resulted in a win and a loss.

### Analysis of lateral canopy spread and tree height

Stratified sampling was necessary to achieve comparable sample sizes for each ant species across tree height classes. Along random transects, we selected one of four target height classes (1–1.99 m, 2–2.99 m, 3–3.99 m,  $\geq 4$  m) at random, and then searched until we found the nearest tree within that height class occupied by each of the plant-ant species.



**Figure 4** Growth asymmetry of *A. drepanolobium* canopies, as a function of ant occupant and the presence of hostile ant colonies on neighbouring trees. A positive value of relative canopy spread indicates disproportionate lateral growth in a given direction. The local neighbourhood within each quadrant centred around a focal tree was categorized as 'different', if a tree bearing a different colony occurred within 3 m; or 'same or none', if no different ant colony occurred within 3 m. Separate ANOVAs were conducted for each ant species; least-square means and standard errors from those models are shown. Double asterisks,  $P < 0.01$ .

The height of the tallest living shoot was measured, and canopy diameter was calculated as the mean of two perpendicular canopy widths. Analysis of covariance was used<sup>27</sup> to determine whether mean canopy spread is predicted by tree height and/or species of ant occupant. For each ant, canopy spread was regressed on tree height and the square of height. The quadratic component was significantly negative for trees occupied by *C. nigricipes* ( $P = 0.0307$ ), but not for trees occupied by the other three ant species ( $P$  ranged from 0.16 to 0.84).

**Analysis of canopy asymmetry.**

Along 10 transects, we randomly selected 555 *A. drepanolobium* trees 1–2 m tall. The lateral canopy spread of each focal tree was measured outwards from its rooting point along the four cardinal directions. In the cardinal quadrants surrounding each focal tree, we measured distance to the nearest neighbouring tree within 3 m, and noted which ant species occupied that neighbour. For *C. nigricipes* and *T. penzigi*, if the neighbouring ant was the same species as that on the focal tree, we experimentally transferred ants between trees and monitored their interactions to determine whether they belonged to different colonies. This assay was not conducted for *C. mimosae* and *C. sjostedti*, as these two species form extensive colonies on many trees, and aggressive interactions between adjacent trees are relatively rare. For each ant species, we conducted ANOVA with cardinal direction and the presence or absence of a neighbouring ant colony as predicting factors. Deviation from canopy symmetry, measured as the difference between lateral spread in one direction and the mean lateral extension for that tree, was the outcome variable.

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**Diet-dependent female choice for males with ‘good genes’ in a soil predatory mite**

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**Female choice for mates with ‘good genes’ presupposes that some males have better genes than others<sup>1</sup>. However, the resulting selection against inferior males causes such genetic variability to disappear. This paradox may be resolved when substantial variability is maintained at a balance between selection and mutation<sup>2</sup>. Alternatively, populations may exhibit genetic polymorphisms maintained by frequency-dependent selection or hybrid vigour<sup>3–9</sup>. Here we show that a local population of soil predatory mites exhibits genetic variation in preference for two prey species. We find that hybrids between selected preference lines are superior or inferior in population growth rate, depending on the composition of the diet. Finally, we show that females in this population mate disassortatively when hybrids are superior, but switch to assortative mating otherwise. Thus, mate choice varies with diet and is tuned to incorporate ‘good genes’ in the offspring, that is, genes that promote the population growth rate of the offspring on the same diet as that experienced by the parents. In this way, hybrid success and mate choice act together in maintaining or eliminating genetic polymorphism in local populations.**

Polyphagy is thought to be widespread among predatory arthropods<sup>10</sup>, but the evidence comes from species- or population-wide pooling of data on prey consumption. To investigate genetic variation in food selection, we studied the small (<1 mm), soil-inhabiting predatory mite *Hypoaspis aculeifer* (Canestrini) (Acari: Laelapidae), which preys on fungivorous and herbivorous mites, insect eggs and larvae (notably beetles, flies, thrips and springtails), enchytraeid worms and nematodes<sup>11,12</sup>. It reproduces by arrhenotokous parthenogenesis, which makes genetic analysis easy because isofemale lines can be created through mother–son mating<sup>11–13</sup>.

We found that a local population of this predatory mite harbours genetic variation in prey choice with respect to two species of astigmatic mites: the bulb mite *Rhizoglyphus robini* Claparède (prey R), and the copra mite *Tyrophagus putrescentiae* (Schrank) (prey T). Predator and prey were collected from a very small area (0.25 m<sup>2</sup>) in a lily field. Both prey species were reared on yeast flakes at 15 °C, and predators were reared on prey T at 22 °C with 70% relative humidity. Prey preference was assessed by subjecting individual females to three two-choice tests. Those exclusively attacking prey R or T were used to start isofemale lines, yielding lines with opposite preferences after four generations<sup>12</sup> (Fig. 1). Analysis of preference in F<sub>1</sub> hybrids and F<sub>1</sub> × parent backcrosses showed that preference is inherited as if determined by a single gene (or several tightly linked genes)<sup>12</sup> (Figs