Guards and thieves: antagonistic interactions between two ant species coexisting on the same ant-plant

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Abstract. 1. The simultaneous occupation of a rare understorey ant-acacia *Acacia mayana* by its guarding ant *Pseudomyrmex ferrugineus*, and an apparent opportunist parasite of the mutualism, the generalist ant *Camponotus planatus* is described. The two ant species occur together in 30.7% of the 26 mature *A. mayana* plants [23.5% of all trees ($n = 34$)] surveyed, but *C. planatus* is absent from saplings below 1 m in height ($n = 8$).

2. While *P. ferrugineus* shows behaviour compatible with effective host-tree defence, *C. planatus* does not attack phytophagous insects and appears ineffective as an ant-guard. *Camponotus planatus* does, however, occupy swollen thorns (pseudogalls) on the host tree, and harvests nectar from extrafloral leaf nectaries. It is proposed that *C. planatus* is a parasite of the *Acacia–Pseudomyrmex* mutualism.

3. *Camponotus planatus* does not harvest the second trophic reward produced by the tree for its *Pseudomyrmex* ant-guards, protein-rich food (Beltian) bodies. *Camponotus planatus* lack the specialised larval adaptations needed to use Beltian bodies as brood food, suggesting that this resource is potentially more resistant to exploitation by generalists than extrafloral nectar.

4. In competition for access to nectaries, *C. planatus* effectively displaced *P. ferrugineus* in 99.8% of encounters. These results suggest not only that *C. planatus* is a parasite of this mutualism, but also that it is able to effectively counteract the aggression shown to other insects by the resident ant-guards.

Key words. *Acacia mayana*, Ant–acacia mutualism, *Camponotus planatus*, exploitation of trophic rewards, extrafloral nectar, opportunist parasite, *Pseudomyrmex ferrugineus*.

Introduction

The abundance of mutualisms in ecological systems introduces a widespread evolutionary temptation to cheat (Herre *et al.*, 1999; Bronstein, 2001a, b; Yu, 2001). Parasites of mutualisms exploit the resources exchanged between reciprocally cooperating partners whilst providing nothing in return. They have the potential to destabilise, even destroy,

mutualisms lacking effective mechanisms to deter exploitation and reinforce mutualistic actions between partners (Boucher, 1985; Bull & Rice, 1991; Bronstein, 1994a, b).

The mutualistic association between myrmecophytes (ant-plants) and ant-guards is one of the classic examples of interspecific cooperation. Despite the wealth of plant species that form such mutualistic associations with ants, only five exploiting parasites have been described: four ant species (Janzen, 1975; McKey, 1984; Young *et al.*, 1997; Yu & Pierce, 1998; Gaume & McKey, 1999; Stanton *et al.*, 1999) and one beetle (Letourneau, 1990). These cheats are able to exclude the mutualistic ant from some proportion of available host plants by exploiting the period in which

cooperating partners separate to disperse before reuniting in the next generation. Most frequently such competitive exclusion of mutualists is achieved at the sapling stage when the canopy is a mosaic of founding ant colonies, often from several species. This results in the canopy of mature trees being occupied by a single ant (either the mutualist or parasite) species at any given time, although appreciable turnover of the resident ant species may occur within the lifetime of an individual tree (Janzen, 1975; Young *et al.*, 1997; Stanton *et al.*, 1999; Palmer *et al.*, 2000). The exclusion of mutualist ant-guards by non-guarding ant parasites frequently leads to considerable reductions in host-plant longevity, and the quality and quantity of resources they provide (Janzen, 1975) and may also result in reduced seed set (Willmer & Stone, 1997). Some parasites of mutualisms show accelerated colony life cycles, promoting precocious production of sexual offspring (Janzen, 1975), which appears to be an adaptation for effective exploitation of host plants as a degenerating resource.

An alternative scenario, in which mutualist and parasitic ant species share the same individual host plant, might enable the parasite to exploit the products of the mutualism for longer because the host plant quality is maintained by the mutualist; however, cohabitation is potentially associated with a significant cost to the parasite – the threat of lethal aggression from the ant-guards. Although multiple ant species are known to co-occupy individual ant-plants (Wheeler, 1942; Davidson & McKey, 1993; Longino, 1996), including ant-acacias (Emery, 1891; Wheeler, 1913; Ward, 1989), none show this type of parasite–mutualist coexistence. Generally these cases document an unusual ant species occupying host plants alongside a well documented ant mutualist, e.g. non-aggressive *Pseudomyrmex subtilissimus* cohabiting with *P. flavicornis* ant-guards on Costa Rican ant-acacias (Ward, 1989). However the interactions between cohabiting ants are rarely studied in sufficient detail to establish whether the second, and frequently less common, ant species represents a mutualist, commensal or parasite of the ant-plant mutualism with which it coexists.

The host plant in this study is *Acacia mayana* Lundell (Mimosoideae, Leguminosae), the rarest neotropical ant-acacia (Janzen, 1974). Beyond a known association with the ant-guard *Pseudomyrmex ferrugineus* (Janzen, 1974), *A. mayana* is virtually unstudied. Preliminary observations showed some individuals to be occupied by two ant species. The first, *Pseudomyrmex ferrugineus* Smith (Formicidae: Pseudomyrmecinae), is a known ant-guard of other neotropical acacias, and is presumed to represent the true mutualist of the two ant species. The second is a wide-ranging generalist arboreal ant, *Camponotus planatus* Roger (Formicidae: Formicinae) (Oliveira *et al.*, 1999). Wheeler (1913) observed the same species pair co-occupying *Acacia cornigera* and *Acacia hindsii* in Guatemala [although he recorded *P. ferrugineus* as *P. fulvescens* (see Ward, 1993)]. Although Wheeler does not describe interactions between the two ant species in detail, he described their cohabitation as a 'peculiar pacific relationship' (parabiotic *sensu* Forel, 1898) suggesting that *C. planatus* represents either a commensal or a second

mutualist in these ant–acacia associations. This investigation represents the first behavioural study of either ant species on *A. mayana*, and the most detailed observations of the common opportunist ant *C. planatus* forming associations with any ant-plant.

Here the interactions between the two ant species are described in detail, focusing in particular on the potential for competition for plant trophic rewards. The following specific questions are addressed: (1) Does the behaviour of *C. planatus* suggest that it is an additional mutualistic ant-guard, or an apparent parasite of trophic rewards provided by *A. mayana*? (2) How do *C. planatus* and *P. ferrugineus* exploit plant-derived food rewards (extrafloral nectar and Beltian bodies) on *A. mayana*, and how do these ant species interact when co-occurring on the same tree? (3) How are the nests of *C. planatus* and *P. ferrugineus* distributed within the crown of co-occupied *A. mayana* trees?

Methods

Ant occupancy of Acacia mayana

The study population of *A. mayana* were located in the understorey of primary and secondary growth forest at the Estación de Biologia Tropical 'Los Tuxtlas' IBUNAM, Veracruz, Mexico (18°57.72'N, 95°04.90'W). *Acacia mayana* individuals of all sizes, located by forest census in July–August 2001, were surveyed to establish which ant species occupied their pseudogalls. Tree height, branch number, and the abundance of leaves and pseudogalls per branch were recorded for each tree. These data were then used to investigate potential differences in ant occupation with respect to plant life stage, and in particular to determine which species first colonised saplings. Two life stages were identified in *A. mayana*: (1) saplings were less than 1 m tall and characterised by narrow, flexible stems and few, if any, side branches, whilst (2) mature individuals were larger (1–5.5 m), had thickened, heavily lignified stems, and considerable primary and secondary branching. During analyses mature trees were divided into 1-m height classes to enable direct comparisons with saplings.

Ant behaviour

Foraging behaviour. Diurnal and nocturnal observations of foraging behaviour were made for both ant species. General activity outside pseudogalls was quantified using instantaneous counts of all the ants visible on five 40-cm branch sections (each containing ant-occupied pseudogalls and leaves) in each of four undisturbed trees (three jointly occupied and one occupied only by *P. ferrugineus*). Hourly counts of ant activity were made for each branch section throughout a 26-h period (06.00–08.00 hours) on two occasions (18–19 and 21–22 July).

In common with all neotropical ant-acacias, *A. mayana* produces two types of trophic reward for its ant-guards: (1)

sugar-rich nectar from extrafloral nectaries on mature leaves, and (2) protein-rich Beltian bodies. Beltian bodies occur on the leaflet tips of new leaves and once removed are not replaced. Rich in protein and lipid, Beltian bodies are used by all *Pseudomyrmex* ant-guards of neotropical ant-acacias as brood food. *Pseudomyrmex* larvae possess a ventral thoracic pouch (trophothylax) into which workers insert Beltian body fragments for the larva to consume (Petralia & Vinson, 1979). *Camponotus planatus* larvae lack this specialisation, raising the question of whether these ants can effectively exploit Beltian bodies as food. The foraging behaviour (described in detail below) of both ant species on three undisturbed trees was investigated, noting which reward was harvested, and whether alternative food sources were harvested either on or off the tree.

Ant interactions at extrafloral nectaries. Pseudomyrmex ferrugineus and *C. planatus* workers were both observed to visit extrafloral nectaries in jointly occupied canopies, leading to frequent interspecific interactions. Nectary encounters between conspecific or heterospecific individuals were categorised as (1) displacement, or (2) non-displacement of the ant(s) resident at the nectary by the approaching individual, or (3) nectary sharing by the resident and approaching ant(s). Nectary interactions were observed between 07.00 and 12.00 hours (for 30 min on the hour), for three trees, on 2 days per tree (6 tree days in total).

The proportion of interactions resulting in each potential outcome (displacement, non-displacement, or sharing) was compared amongst interaction types (interaction types given in the form: resident–approacher: P–P, P–C, C–P, C–C, where P = *P. ferrugineus* and C = *C. planatus*) using a Chi-squared test, to test whether outcome frequency depended on interaction type. It was subsequently tested whether either species of resident ant would be more likely to be displaced by a conspecific or a heterospecific approacher.

Extrafloral nectar secretion

Nectar secretion rates were quantified by analysing changes in nectar standing crop over time from extrafloral nectaries on leaves from which ants were excluded using banding grease (Raine *et al.*, 2002). All nectaries on a leaf were emptied every 15 min with a 1-μl micropipette (Camlab, Cambridge, U.K.), and the nectar volume calculated from the length of the nectar column. A set of 18 leaves was sampled for one tree on three non-consecutive days, with additional data collected from a second tree on a further day.

Results

Ant occupancy of Acacia mayana

All trees censused ($n = 34$) contained ant-occupied pseudogalls: 26 trees (76.5%) were occupied exclusively by *P. ferrugineus*, whilst eight (23.5%) were jointly occupied by *P. ferrugineus* and *C. planatus*. *Camponotus planatus* workers were present in the canopies of mature trees in each 1-m height category (1–4 m tall), but were absent from saplings. *Camponotus planatus* colonies in jointly occupied trees were always smaller than the resident *P. ferrugineus* colony: estimates based on maximum counts of workers outside pseudogalls on undisturbed trees suggest that *P. ferrugineus* colonies were 8.1 ± 2.6 times larger; however, as no trees were sampled entirely these estimates of relative size must be regarded as preliminary.

Despite apparently smaller colonies, *C. planatus* occupied pseudogalls on $53.6 \pm 8.0\%$ of the branches in each jointly occupied tree. The majority of these branches were occupied by both ant species, with only $5.4 \pm 2.8\%$ being occupied exclusively by *C. planatus* (Fig. 1). In all shared canopies surveyed, each ant species inhabited separate pseudogalls.
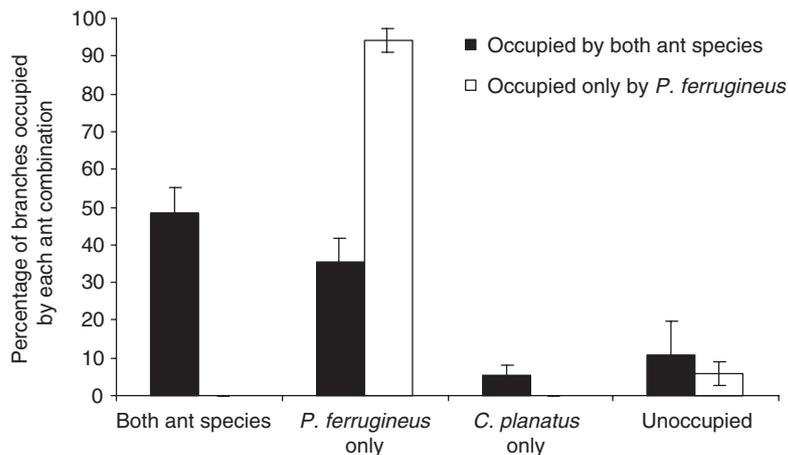

Fig. 1. Percentage of canopy occupied by *Pseudomyrmex ferrugineus* and *Camponotus planatus* in solely ($n = 26$: *P. ferrugineus* only) and jointly ($n = 8$) occupied *Acacia mayana* trees. For each branch within a tree canopy, all pseudogalls were assessed for ant occupancy leading to the branch being classified as (1) *unoccupied*, or occupied by either (2) *P. ferrugineus* or (3) *C. planatus*, or (4) both species simultaneously. Error bars represent ± 1 S.E.

Pseudomyrmex ferrugineus preferentially occupied pseudo-galls near shoot tips. *Pseudomyrmex* colonies track the growth of their host plant; moving pseudogalls to remain near the new leaves and their Beltian bodies (Raine *et al.*, 2002). Therefore, old and/or damaged pseudogalls are routinely abandoned even in the absence of parasites. Terminal pseudogalls were not occupied by *C. planatus*, which were most frequently observed occupying the oldest and/or most damaged pseudogalls on host trees. These pseudogalls had considerably enlarged entrance holes compared to those occupied by *P. ferrugineus*. This suggests that *C. planatus* workers are unable to enter *P. ferrugineus* occupied pseudo-galls, and only occupy pseudogalls already vacated by *P. ferrugineus* by enlarging the entrance hole.

Ant behaviour

Foraging behaviour. *Pseudomyrmex ferrugineus* colonies showed high levels of activity throughout the canopy. Appreciable numbers of workers actively patrolled the canopy throughout the day and night (Fig. 2). In contrast, *Camponotus planatus* activity was predominantly diurnal and concentrated close to nest pseudogalls. Large numbers of ants from both species visited extrafloral nectaries to collect nectar. Nectar secretion occurred in a discrete daily pulse (09.00–12.00 hours: Fig. 3a), coinciding with visitation by both species (Fig. 3b). *Pseudomyrmex ferrugineus* workers also harvested Beltian bodies throughout the day (09.00–19.00 hours), transporting them to their pseudogalls. *Camponotus planatus* workers very rarely visited leaves bearing Beltian bodies, and neither removed them, nor consumed them in situ.

Ant interactions at extrafloral nectaries. The majority of interspecific ant interactions occurred at nectaries, with out-comes summarised in Fig. 4. The proportion of interactions resulting in each outcome (displacement or non-displacement of the resident by an approacher, or nectary sharing) was significantly dependent on the combination of ants involved in the interaction ($\chi^2_6 = 1870$, $P < 0.0001$). *Pseudomyrmex ferrugineus* workers were significantly more likely to be displaced from a nectary when approached by *C. planatus* compared to a conspecific ($\chi^2_1 = 1108$, $P < 0.0001$). In contrast, *C. planatus* workers were significantly less likely to be displaced from a nectary by *P. ferrugineus* than by a conspecific ($\chi^2_1 = 113$, $P < 0.0001$).

The vast majority (99.8%) of heterospecific encounters at nectaries involved conflict, resulting in the displacement (*P. ferrugineus*) or non-displacement (*C. planatus*) of the resident ant. While physical contact by antennation was common, no individual of either species exhibited aggressive behaviour towards heterospecific workers, irrespective of whether a *resident* or *approacher*. *Camponotus planatus* workers displaced resident *P. ferrugineus* workers even when walking up behind them, often only contacting the *Pseudomyrmex* ant's gaster with their antennae. Nectary sharing by both species was extremely uncommon ($< 0.2\%$ of interactions), but was relatively frequent amongst conspecifics (9–15% of interactions).

Discussion

Camponotus planatus colonies persist on mature *A. mayana* plants despite the presence of larger *P. ferrugineus* colonies, and their workers effectively exclude *P. ferrugineus* from nectaries. This suggests that *C. planatus* persists alongside *P. ferrugineus* as a result of competitive superiority in interspecific encounters rather than through avoidance of confrontations.
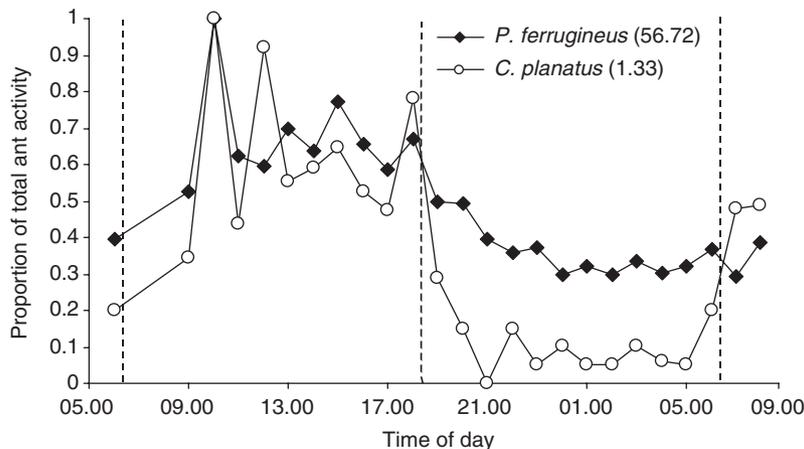

Fig. 2. Daily activity patterns of *Pseudomyrmex ferrugineus* and *Camponotus planatus* in the canopy of *Acacia mayana*. Activity was quantified using instantaneous counts of ants outside pseudogalls on five 40-cm branch sections in each of four undisturbed trees (three jointly occupied and one occupied only by *P. ferrugineus*). Both data sets have been constrained to vary between 0 and 1 for ease of interspecific comparison, with the scaling values given in parentheses for each data set in the relevant key to plotting symbols. The vertical dashed lines indicate the timings of sunrise and sunset over this 26-h period.
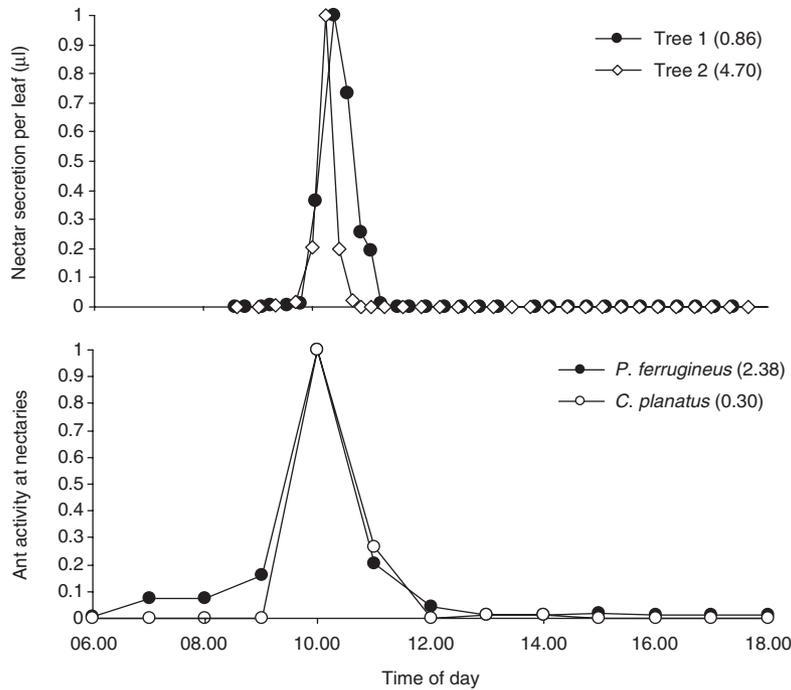
Fig. 3. Daily patterns of nectar secretion and harvesting from extrafloral nectaries of *Acacia mayana*. (a) Mean nectar secretion rates per leaf (microlitres secreted in 15 min) for two *A. mayana* individuals (means are over 3 days for tree 1 and 1 day for tree 2). (b) Mean instantaneous counts of ants of each species (*Pseudomyrmex ferrugineus* or *Camponotus planatus*) observed collecting nectar from extrafloral nectaries per leaf. Means for each ant species were calculated between two trees on 2 days per tree (on each day 27–36 leaves were observed per tree). As for Fig. 2, data sets have been constrained to vary between 0 and 1 with the scaling values given in parentheses for each data set in the relevant key to plotting symbols.

Is Camponotus planatus *a mutualist or a parasite of* Acacia mayana?

Could *C. planatus* represent an alternative ant-guard of *A. mayana*, potentially complementing (or replacing)

P. ferrugineus? *Camponotus planatus* workers avoided confronting herbivores encountered in the canopy suggesting that, unlike *P. ferrugineus*, they are unlikely to repel herbivores directly. Non-aggressive ant-guards can effectively reduce herbivore damage by disrupting herbivore feeding (De la
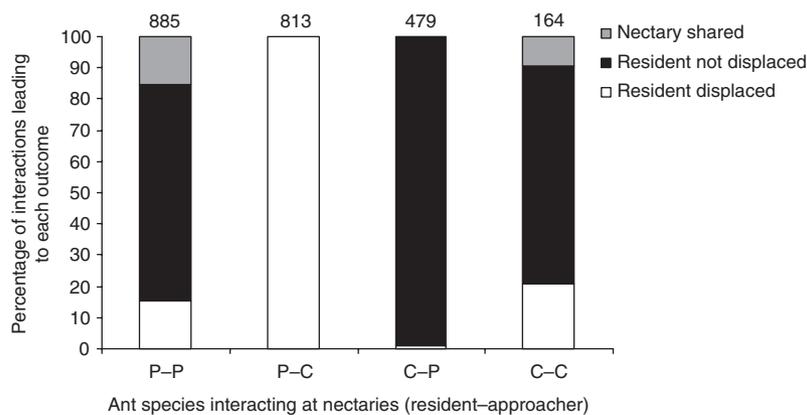

Fig. 4. Outcomes of ant interactions at the extrafloral nectaries of *Acacia mayana*. The mean proportion of interactions resulting in each outcome (displacement, non-displacement, or nectary sharing) is presented for each of the categories of ant interaction (resident–approacher: P–P, P–C, C–P, C–C, where P = *Pseudomyrmex ferrugineus* and C = *Camponotus planatus*) across all trees and days. Data were collected for three trees on 2 days per tree (6 tree days in total), and averaged firstly for each tree between days, then across trees. Total numbers of interactions observed for each ant interaction category are given above each column.

Fuente & Marquis, 1999) and/or remove eggs and larvae of phytophagous insects (Letourneau, 1983; Gaume *et al.*, 1997); however, *C. planatus* workers were never seen removing eggs or disrupting feeding phytophagous insects. To be effective, passive ant-guards must patrol their host plant; however, *C. planatus* workers were rarely observed >5 cm from their pseudogall except when harvesting nectar. Even then *C. planatus* workers only visited nectaries along the leaf midrib and did not patrol the rest of the leaf. Though more detailed analyses of *C. planatus* foraging are required, temporal and spatial patterns described here do not suggest they are effective ant-guards. The behaviour and larval morphology of *P. ferrugineus* suggests that these ants are the true coevolved mutualistic ant-guards of *A. mayana*. If true, then any cost imposed by *C. planatus* on *P. ferrugineus* also imposes a parasitic cost on *A. mayana*.

Camponotus planatus could impose two potential costs on *P. ferrugineus*: reduced availability of (1) *Acacia* trophic rewards and (2) nest space. *Camponotus planatus* do not compete for Beltian bodies – the primary protein source for *P. ferrugineus*. The inability of *C. planatus* to exploit this resource may be due to the absence of a trophothylax in its larvae. If so, *Acacia–Pseudomyrmex* coevolution may have produced a means of resource transfer resistant to exploitation by distantly related ant taxa (Yu, 2001). However, harvesting nectar requires no such morphological specialisation, and *A. mayana* nectar still appears to represent a valuable trophic resource for *C. planatus*. *Camponotus planatus* actively displaces *P. ferrugineus* from nectaries, and so reduces local nectar availability. If it is assumed that *C. planatus* is not an effective ant-guard of *A. mayana*, then whether it is a parasite or a commensal depends on the impact of competition for nectar on the *Pseudomyrmex* colony. *Pseudomyrmex ferrugineus* ants always recruit rapidly to nectaries following the onset of extrafloral nectar secretion (Raine *et al.*, 2002; N. E. Raine, N. Gammans, I.J. MacFadyen, G.K. Scrivner, A.S. Pierson and G.N. Stone, unpubl. data) strongly suggesting that nectar is a valuable resource and hence that it may be limiting. Further experimental analysis on the impact of nectar availability on ant-guard colony growth and activity is required to quantify this effect.

Even as sole canopy occupants *P. ferrugineus* do not occupy all available pseudogalls, preferentially occupying those closest to the new growth (Raine *et al.*, 2002), and move from older to younger pseudogalls as the canopy grows. The occupation of older pseudogalls by *C. planatus* may simply represent colonisation of thorns abandoned by *P. ferrugineus*, in which case no cost is imposed. Longer term studies of pseudogall occupation by *C. planatus* are required to test this hypothesis.

How is occupation of Acacia mayana *by* Camponotus planatus *initiated and maintained?*

The colonisation patterns of the two ant species on *A. mayana* appear to differ considerably. *Pseudomyrmex ferrugineus* colonies were found in all plants examined irrespective of their size, whereas *C. planatus* colonies were found in approximately 30% of mature trees, but not in saplings. While further sampling is required to confirm the absolute absence of *C. planatus* colonies from saplings, if true the pattern may indicate either an inability of *C. planatus* queens to excavate pseudogalls *de novo*, or their competitive displacement by *P. ferrugineus* foundresses. The generalist cavity nesting behaviour of *C. planatus* in habitats other than *Acacia* trees suggests that this species may lack the specific behaviours necessary to excavate pseudogalls. The alternative – exclusion of *C. planatus* by *P. ferrugineus* – seems unlikely given observations of competition at nectaries, in which *C. planatus* is almost always superior. However, it is also possible that the more limited resources available on very small trees either make them less attractive to *C. planatus* queens, or cause *P. ferrugineus* colonies to be less tolerant of them. These hypotheses will be tested in future work on this system.

In most neotropical ant-acacias, highly aggressive ant-guards appear sufficient to exclude potential ant parasites of their mutualism. Yet *C. planatus* colonies persist in *P. ferrugineus* occupied trees exploiting both pseudogalls and nectar. It has been suggested that ants with sting-based defences (e.g. *Pseudomyrmex*) may be generally inferior to those chemically defended species (e.g. *Camponotus*) in aggressive confrontations (Davidson *et al.*, 1988). It is thus possible that release of formic acid explains the dominance of *C. planatus* at nectaries; however, no evidence was seen to support this hypothesis. During interspecific interactions *C. planatus* workers did not adopt the characteristic posture (gaster swung forward beneath the thorax with its tip facing forwards) associated with release of formic acid. If *C. planatus* did release formic during such interspecific interactions, it would be expected for *P. ferrugineus* workers to show an obvious alarm response, and avoid the nectary for at least a short while afterwards. Neither was observed.

It is hypothesised that *C. planatus* are able to modify the normally aggressive behaviour of *P. ferrugineus* through chemical mimicry of intraspecific communication signals as in other parasites of ants (Allan & Elgar, 2001). This would allow *C. planatus* to exploit host-produced trophic rewards, whilst receiving protection from true ant-guards. *Pseudomyrmex ferrugineus* may be caught in a sensory trap (Christy, 1995) whereby *C. planatus* hijack their normal behavioural responses using chemical mimics of signals essential to *Pseudomyrmex* intraspecific communication. Manipulation of the behaviour of ant-guards by their hosts has been demonstrated in both American and African ant-acacia mutualisms (Willmer & Stone, 1997; Ghazoul, 2001; Raine *et al.*, 2002). The facultative nature of *A. mayana* occupation by *C. planatus* makes it difficult for either mutualist to evolve effective countermeasures because *C. planatus* can simply vacate the tree and nest elsewhere. If the sensory manipulation hypothesis is true, this raises the question of how a generalist ant, without obligate associations with the *Acacia–Pseudomyrmex* system, has evolved an apparently specialist behavioural modification of a

specific ant-guard. If this were a general *Camponotus* trait it might be expected to find them associated as parasites of more ant-plant mutualisms. The absence of such relationships suggests instead that this system represents a chance convergence in volatile signals used rather than a complex coevolved manipulation of ant-guards.

Acknowledgements

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