Not all ants are equal: obligate acacia ants provide different levels of protection against mega-herbivores

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Abstract

In obligate ant–plant mutualisms, the asymmetric engagement of a single plant species with multiple ant species provides the opportunity for partners to vary in their behaviour. Variation in behaviour has implications for the interactions with third-party species such as herbivores. This study assessed the effect of obligate ant-mutualists (*Crematogaster mimosae*, *Crematogaster nigriceps* and *Tetraponera penzigi*) inhabiting the African ant-acacia (*Acacia drepanolobium*) on three mega-herbivore browsers: the Maasai giraffe (*Giraffa camelopardalis tippelskirchi*), the reticulated giraffe (*Giraffa c. reticulata*) and the black rhino (*Diceros bicornis*). Giraffes are abundant and wide-ranging herbivores of the acacias, whereas black rhinos are localized and perennial herbivores of the acacias. Multiyear field studies comparing the ants' aggressive behaviour and browsing by mega-herbivores suggested differences between the tending abilities of the primary ant species inhabiting *A. drepanolobium*. Trees occupied by the aggressive ant species *C. mimosae* had significantly less browsing by giraffes and black rhino than trees occupied by other ant species. The results of this study provide evidence that ant-mutualists on African acacias can serve as deterrents to mega-herbivores and that different ant species vary in their tending abilities.

Key words: Acacia drepanolobium, ant–plant interactions, black rhino, *Crematogaster*, giraffe, *Tetraponera*

Résumé

Dans des mutualismes restreints – ou symbioses – fourmis-végétaux, l'engagement asymétrique d'une seule espèce végétale avec de multiples espèces de fourmis offre aux partenaires la possibilité de faire varier leur comportement. La variation du comportement a des implications pour les interactions avec des espèces tierces telles que les herbivores. Cette étude évalue l'effet de fourmis (*Crematogaster mimosae*, *C. nigriceps*, *Tetraponera penzigi*) vivant en symbiose sur l'acacia africain *Acacia drepanolobium* sur trois mégaherbivores: la girafe masaï *Giraffa camelopardalis tippelskirchi*, la girafe réticulée *Giraffa c. reticulata* , et le rhino noir *Diceros bicornis.* Les girafes sont abondantes et ce sont des consommateurs très répandus des acacias, alors que les rhinos noirs sont des consommateurs permanents et très localisés. Des études de plusieurs années portant sur le caractère agressif des fourmis et sur la consommation des mégaherbivores ont suggéré des différences entre les capacités de protection des premières espèces de fourmis habitant *A. drepanolobium.* Les arbres occupés par l'espèce de fourmi agressive *C. mimosae* étaient sensiblement moins consommés par les girafes et par les rhinos noirs que ceux qui étaient occupés par d'autres espèces de fourmis. Les résultats de cette étude donnent des preuves que les fourmis mutualistes des acacias africains peuvent servir de répulsifs pour les mégaherbivores et que la capacité de protéger les arbres varie selon les différentes espèces de fourmis.

Introduction

Ant–plant mutualisms are a widespread feature of the tropics (Mckey, 1984; Beattie, 1985; Davidson & Mckey, 1993; Heil & Mckey, 2003). Ant-mutualists protect the plants against herbivory, including by phytophagous insects (Janzen, 1966) and mammalian browsers (Madden & Young, 1992) and in some species can reduce competition with other plants (Frederickson, Greene & Gordon, 2005). In ant–plant mutualisms, both partners also interact with other species. Cooperating or cheating within

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the mutualism may influence interactions with these third-parties, such as herbivores, through antagonistic or other interactions with the ants and plants (Bronstein, 2001; Ehrlich & Raven, 1965; Heithaus, Culver & Beattie, 1980; Price *et al.*, 1980; Thompson, 1994; Thompson, 2005).

Ant–plant mutualisms typically involve a single plant species inhabited by a number of different ants (Holldobler & Wilson, 1990; Jolivet, 1996). These ant inhabitants have all been classified as 'mutualists' in the sense that they can be seen patrolling the plant and in most cases, appearing to protect it against herbivores (Janzen, 1966; Madden & Young, 1992; Young, Stubblefield & Isbell, 1997; Palmer, Stanton & Young, 2002; Stanton, 2003; Palmer *et al.*, 2007). Different species may vary in the benefits they provide for their host plant, with some species being excellent tenders, and others effectively being parasites of the mutualism (Janzen, 1975; Yu & Pierce, 1998); however, parasitism has rarely been shown clearly (Sachs & Simms, 2006). Poor tenders (cheaters) in a mixed population can exploit the plant, while strong tenders perpetuate the mutualism. Cheating by ants (through not providing tending services) can influence both facultative and obligate ant–plant associations (Sachs *et al.*, 2004).

The results presented here build on the long-term ecological studies conducted at a site near Laikipia in northern Kenya that has been intensively studied. These studies have emphasized competition and colonization dynamics between different ant species in this system resulting in dominance hierarchies between different ant inhabitants occupying *Acacia drepanolobium* Harms (Young, Stubblefield & Isbell, 1997; Stanton *et al.*, 1999; Palmer, Young & Stanton, 2000; Palmer, Stanton & Young, 2002; Palmer, 2003; Palmer & Brody, 2007; Palmer *et al.*, 2007). Previous studies have hinted at differential repulsive abilities of African acacia ants (Hocking, 1970), and several have suggested that there are systematic differences between species (Madden & Young, 1992; Young, Stubblefield & Isbell, 1997; Palmer, Stanton & Young, 2002; Palmer, 2003; Palmer *et al.*, 2007). The Madden & Young (1992) of giraffe browsing patterns showed that young giraffes browsed less on trees with *Crematogaster* ants. An experimental study using goats looking at the effects of ants versus thorns also found evidence of ants being effective against herbivory (Stapley, 1988). African studies of herbivory have primarily emphasized the interaction of large, grazing and browsing mammals with vegetation (Stapley, 1988; Shorrocks, 2007), so the work here deliberately set out to investigate the effect of ant-mutualists on browsers.

The interactions of ant–plant inhabitants with two kinds of large browsing ungulates, the giraffe and the black rhino are explored here. The focus of this study differs from previous work by providing a fine-scale analysis of the behaviour/response of different ant species and their abilities to deter herbivores. This study also investigates whether herbivores detect and respond selectively to different inhabitant ant species. These interactions can have important ecological implications in this ecosystem, as many East African acacias are adapted for recruitment of ants.

Materials and methods

Study sites

This research was conducted at two savannah sites in Kenya. For the giraffe, two main localities were used over the period of the study: Kajiado North District 'Kitengela' (36°49′ E, 1°23′ S; 1660- m elevation) and Suyian in Laikipia (36°42′ E. 0°32′ N; 1820 m elevation). The Maasai giraffe data were collected in the seasonal semi-arid Kajiado ecosystem in south-central Kenya where *A. drepanolobium* is a common feature of the vegetation, forming large, dense near mono-dominant stands on high-altitude grasslands. Data for the reticulated giraffe were collected from extensive stands of *A. drepanolobium* found on Suyian Ranch in Laikipia District, north of where the previous long-term studies have been carried out (Madden & Young, 1992; Young, Stubblefield & Isbell, 1997; Palmer, Stanton & Young, 2002; Stanton, 2003; Palmer & Brody, 2007). All Black Rhino data were gathered from *A. drepanolobium* stands in Nairobi National Park and the dispersal area (a migratory corridor between the Nairobi National Park and the adjacent ecosystem) consisting of savannah and grassland (used primarily by ungulates) close to the Mbagathi River.

Natural history of the system

Studies have documented four principal ant-mutualists of *A. drepanolobium* in Laikipia, northern Kenya (Madden & Young, 1992; Young, Stubblefield & Isbell, 1997; Palmer, Stanton & Young, 2002; Stanton, 2003; Palmer & Brody, 2007), and their vertical spatio-temporal patterns of host tree occupancy (Young, Stubblefield & Isbell, 1997). Both the Kitengela (Kajiado) and the Suyian (Laikipia) study sites have three of these four species in high numbers:

Crematogaster mimosae Santschi, *C. nigriceps* Emery and *Tetraponera penzigi* Mayr. All the ant-mutualists depend on the domatia provided by the plant for brood rearing and appear to be obligate symbionts of the trees in the sense that colonies of these ants are never found free living separately from the acacias. Ants patrol all parts of the tree above the ground and can therefore directly prey on invertebrates and repel browsing herbivores (Hocking, 1970).

Experimental design

To assess the overall abundance and distribution of acacia ants, they were identified occupying trees along 20 linear 200- m transects running in an east–west direction at each site. This data represented the naturally occurring proportions of trees with different ant spp. available at each site. These data were used to establish the predicted browsing of a giraffe, if it was browsing in a random (i.e. indiscriminate) pattern. The occurrence of other acacia species not associated with ants (*Acacia kirkii* Harms, *Acacia mellifera* Benth., *Acacia brevispica* Harms and *Acacia senegal* Willd.) was also collected at each site. These occurred in much lower numbers, relative to the dominant *A. drepanolobium,* and for observation purposes were lumped together as nonobligate ant-associated 'other acacias'. The timing of the study was done to coincide with peak growth and ant-activity as well as the presence of browsers in the ecosystem. Observations were made in the months of June–August of each year. At this time, all trees are in full leaf and good condition and therefore, other than for ant presence, equally available and attractive to herbivores. All ants are also active at this time of year, and the mutualism is at its peak with ants patrolling and the tree providing extra-floral nectar rewards (Hocking, 1970).

Assessing the browsing patterns of giraffe and their response to ants

Observations of giraffe browsing were made broadly within the sites where the distribution of ants had been previously determined. Data were collected from two different subspecies of giraffe. The Maasai giraffe is found in southern and eastern Kenya, including the Nairobi National Park, while the reticulated giraffe is found in northern Kenya (Kingdon, 2004). Data on giraffe browsing patterns and ant response were collected in two ways from free-ranging giraffes in natural areas:

1 Individual giraffes were followed for time periods of ∼3 h each as they browsed on acacias. The numbers of trees browsed on and the species of ant present were recorded. When a giraffe moved away from a tree, the part of the tree browsed was inspected, and the number (estimate of the number of ants swarming over the area that had been browsed by the giraffe) and type of ants present recorded (N = 30 giraffes – Kajiado, N = 32 giraffes – Laikipia). This was performed within 2–3 min of a giraffe departing from browsing at an individual acacia.

2 The ant species distributions were mapped for stands of *A. drepanolobium,* in areas frequented by giraffe at both sites. Giraffes browsed in these stands as they move between the dispersal area of the Athi-Kapiti-Kajiado plains and the riverine gallery acacia woodlands of Nairobi National Park. In these stands, individuals were monitored more closely. The time spent 'approaching,' i.e. reaching towards, actually browsing on and the identity of the ant species resident on that tree recorded (N = 23 giraffes – Kitengela, N = 29 giraffes – Suyian). This was conducted to test whether giraffe are able to detect the type of ant present on the tree before they decide browse on it. Given the fluid social structure of the giraffe (Estes, 1991) and seasonal movements of ungulates in this ecosystem (Owaga, 1975) as well as by efforts to identify individuals from their distinctive markings, data were not recorded from the same individual more than once. Giraffe data were collected between June and July of each year to coincide with peak activity and full leaf growth. Maasai giraffes were observed in the June–July of 2006 and 2007, and the reticulated giraffe in June–July of 2008 and 2009.

Assessing the browsing patterns of black rhino and their response to ants

Data of overall ant abundance in each site were used to establish predictions for what proportions of ant species inhabiting acacias a black rhino (*Diceros bicornis*) would encounter if browsing in a random (i.e. indiscriminate) pattern. Data for black rhino browsing patterns and ant response were collected in a slightly different manner from that of the giraffe owing to the danger posed by following black rhino. Careful observations were made of the ant-distribution patterns in stands frequented by black rhino. Observations of browsing individuals were made from a stationary vehicle through binoculars and matched with the ant patterns. Ants were identified by a rough mapping of the area on foot during the middle of the day on foot

when no rhinos were present and aided by the use of binoculars and the unique acacia morphology produced by each ant (Stanton *et al.*, 1999). As with the giraffes, efforts were made to limit recording from the same individual. As rhino are rare and more resident and territorial, this resulted in a limited sample (N = 25). Individual rhino are relatively well known at this site because of monitoring by rangers as part of the regular 'rhino patrols' (Kenya Wildlife Service pers. comm.) and have more localized ranges. Therefore, browsing data were matched to individual rhinos. Black rhino data were collected between June 2006 and December 2009.

Statistical analysis

A chi-square test compared browsing by each mega-herbivore across ant species (Tables 1 and 2). The numbers of trees available to a browser with a particular ant spp. (predicted abundance) versus the actual number browsed with the same ant spp. (observed abundance) was tested. Alpha for the chi-squared test was set at $P < 0.05$. The analysis was carried out separately for the two giraffe subspecies and the black rhino. To look at differences in browsing patterns between ant spp., an analysis of variance (ANOVA) was performed with the continuous variable being the mean number of ants recorded responding to the browsing and the categorical variable being the species of ant. A Bonferroni *post-hoc* test was then performed to test for differences between different ant species. The test for differences in response between ant spp. and time spent browsing was performed for the two giraffe subspecies only as responding ant numbers and browsing time were not

recorded for black rhino. To establish whether giraffe were able to discriminate between different ants before they browsed on a tree, an ANOVA of the time spent approaching by different ant spp. was conducted. To look at differences in browsing patterns between ants, an ANOVA of the time spent browsing by the giraffes was conducted with time being the continuous variable and the categorical variable being the species of ant. Alpha for all these tests was set at $P < 0.05$.

Results

Maasai and reticulated giraffe browsing patterns and response by ants

Results were similar for both subspecies of giraffe from the open browsing data. *Crematogaster mimosae* was most effective at limiting browsing by giraffes at both Kajiado and Suyian. Giraffes browsed less on trees with *C. mimosae* and *C. nigriceps.* Giraffes browsed more on trees with *T. penzigi* and nonant associated acacias than would be predicted given their different relative abundances (Table 1). Results for *T. penzigi* were significantly higher for the Maasai giraffe ($P < 0.001$) indicating more browsing than predicted and not significant for the reticulated giraffe ($P = 0.100$) indicating no differences, and therefore no aggressive response by this ant (Table 1). Analysis of browsing patterns from the stands supported these results. There were significant differences between ants in both Maasai (ANOVA $F_{3,124} = 22.7$ $P < 0.0001$) and reticulated giraffe (ANOVA $F_{3,116} = 24.0$ $P < 0.0001$) browsing patterns.

Table 1 Results of giraffe browsing patterns on *Acacia drepanolobium.* The chi-squared test is a comparison of the significance of difference between the predicted and observed (within each ant category) browsing patterns of giraffe

Giraffe subspp.	Ant species/tree	Mean # of ants recruited (±SD)	Predicted browsing (%)	Observed browsing (%)	Chi-statistic X^2	P
Maasai giraffe	*Crematogaster mimosae*	94.3 (13.6)	48.8	32.3	729.4	<0.001
(N = 30)	*Crematogaster nigriceps*	64.2 (9.32)	33.8	17.8	229.8	<0.001
	Tetraponera penzigi	12.1 (5.97)	12.4	20.5	15.3	<0.001
	Other acacias[a]	0.67 (1.15)	5.1	29.4	300.6	<0.001
Reticulated	*C. mimosae*	93.75 (13.44)	53.05	18.1	722.7	<0.001
giraffe (N = 32)	*C. nigriceps*	66.41 (11.52)	31.70	35.06	100.05	<0.001
	T. penzigi	12.66 (5.95)	11.04	19.51	0.16	<0.100
	Other acacias[a]	0.84 (1.37)	4.21	27.33	576.7	<0.001

[a]These are *Acacia mellifera, Acacia kirkii* and *Acacia senegal,* in Kajiado, and *A. mellifera* only in Laikipia, as each of these bears extra-floral nectaries, there were a few facultative ants present on the plants. No *A. drepanolobium* were included in these.

Table 2 Results of black rhino (N = 25) browsing patterns. The chi-squared test is a comparison of the significance of difference between the predicted and observed browsing patterns (within each ant category) of the black rhino

Ant species/tree	Predicted browsing (%)	Observed browsing (%)	Chi-statistic X^2	P
Crematogaster mimosae	50.8	18.3	805.7	<0.001
Crematogaster nigriceps	33.2	39.7	234.2	<0.001
Tetraponera penzigi	12.7	28.9	11.04	<0.001
Other acacias[a]	3.3	13.09	10.7	<0.001

[a]There were only a few *Acacia brevispica* and *Acacia mellifera* at the ant-acacia sites where black rhino were browsing.

For the Maasai giraffe, the Bonferroni *post-hoc* test showed significant differences between *C. mimosae* and other acacias without ants ($P < 0.001$) and between *C. mimosae* and *T. penzigi* ($P < 0.004$). For *C. nigriceps,* results were not significant in comparison with *T. penzigi* ($P = 0.33$) but were significantly different from other acacias without ants ($P < 0.006$). *Tetraponera penzigi* also differed significantly in amount of browsing relative to other acacias ($P < 0.0001$). For the reticulated giraffe, the Bonferroni *post-hoc* test indicated significant differences between *C. mimosae* and both other ant spp. as well as other acacias without ants ($P < 0.001$). For *C. nigriceps,* results were not significant in comparison with *T. penzigi* ($P = 0.24$) but were significantly different from other acacias without ants ($P < 0.03$). This is interesting in that *C. nigriceps* accounts for 32% of trees versus 11% for *T. penzigi,* but the data suggest that browsing patterns were not distinct between the two. *Tetraponera penzigi* also differed significantly in amount of browsing relative to other acacias ($P < 0.02$). Numbers of ants responding (Table 1) to browsed areas differed significantly between ant spp. for both the Maasai (ANOVA $F_{3,124} = 708.3$ $P < 0.0001$) and reticulated giraffe (ANOVA $F_{3,116} = 747.5$ $P < 0.0001$), indicating differences in behaviour between ants.

The observations from the stands where ants were mapped showed that the both giraffes spent similar amounts of time in approaching individual acacias trees, but browsed less from those with aggressive *C. mimosae* (Figs 1 and 2). There were no significant differences in time spent approaching trees with different ant spp. for both the Maasai giraffe (ANOVA $F_{2,66} = 0.36$ $P = 0.7$) and the reticulated giraffe (ANOVA $F_{2,84} = 1.93$ $P = 0.15$), suggesting that both giraffe are not able to recognize ants before they begin browsing. For time spent browsing, there were significant differences on trees with different ants for the Maasai giraffe (ANOVA $F_{2,66} = 19.2$ $P < 0.0001$). This suggests that ants respond to giraffe browsing and affect the time the giraffe spends browsing through their
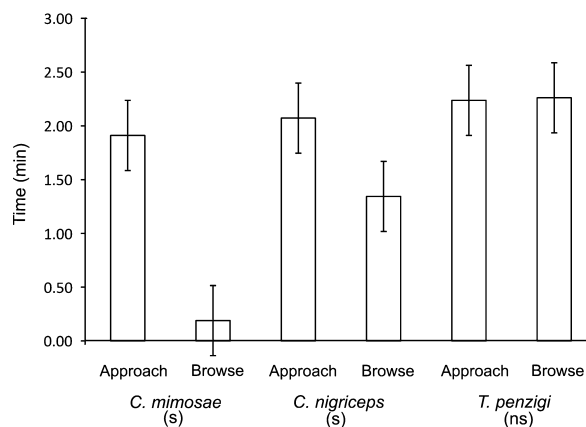

Fig 1 Time spent browsing by Maasai giraffes on *Acacia drepanolobium* inhabited by different ant species (mean ± SE)

aggressive behaviour. *Crematogaster mimosae* differed strongly in the time its trees were browsed when compared to the other two ant spp. ($P < 0.0001$), and *C. nigriceps* also differed significantly from *T. penzigi* ($P < 0.03$). For the reticulated giraffe, there were significant differences in time spent browsing (ANOVA $F_{2,84} = 18.4$ $P < 0.0001$), with *C. mimosae* differing significantly from the two other ant spp. ($P < 0.0001$), and *C. nigriceps* also differed from *T. penzigi* ($P < 0.015$).

Differences in black rhino browsing patterns and response by ants

Black rhino browsed less on trees with *C. mimosae* than would be predicted based on their abundance, and more on other ant spp. (Table 2). There were significant differences in browsing patterns between ants by black rhino (ANOVA $F_{3,92} = 19.9$ $P < 0.0001$). Black rhino browsed less on trees with *C. mimosae* when compared to *C. nigriceps* ($P < 0.0001$) and *T. penzigi* ($P < 0.005$) but did not differ significantly from browsing on other acacias without ants within the stand ($P = 0.057$). As acacias without ants
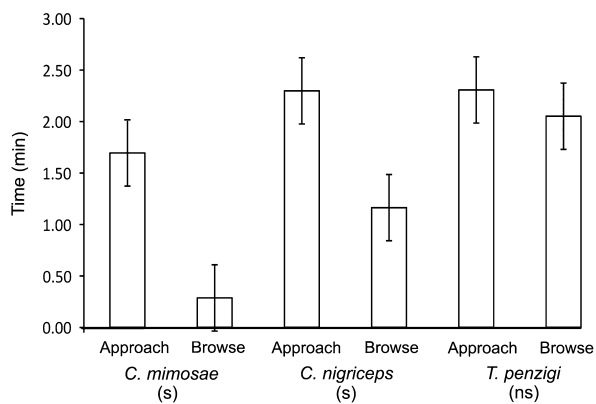
Fig 2 Time spent browsing by reticulated giraffes on *Acacia drepanolobium* inhabited by different ant species (mean ± SE). Note: (s) indicates significant differences and (ns) indicates no significant differences between approach and browse time within each ant spp. based on *post-hoc* tests

composed only 3% of the trees available versus 51% of trees with *C. mimosae*, this indicates that *C. mimosae* was browsed much less by black rhino than predicted given its relative abundance. *Crematogaster nigriceps*-occupied trees were browsed at higher levels than based on their predicted abundance (Table 2) and differed significantly from *T. penzigi* ($P < 0.0022$) and other acacias ($P < 0.0001$). *Tetraponera penzigi* also differed significantly from other acacias ($P < 0.0001$).

Discussion

Different ant species differ in their tending abilities on *A. drepanolobium*. This study suggests that the aggressive ant-guards *C. mimosae* and *C. nigriceps* are effective at limiting browsing by giraffe and black rhino on *A. drepanolobium*. The results here suggest that giraffe alter their behaviour accordingly once engaged in browsing depending on the ant spp. inhabiting the tree. *Crematogaster nigriceps* was a variable defender, sometimes aggressive and sometimes similar to *T. penzigi,* which was not effective at deterring browsers. The black rhino was eventually repelled by aggressive ants, though it was observed that black rhino spent more time browsing from trees before they 'realized' that there were aggressive *C. mimosae* present, then often snorted to dislodge ants from their nostrils before moving on (although the time spent browsing needs to be measured in future studies). This is similar to the effect observed on young giraffes in the earlier study of browsers and ants (Madden & Young,

1992). Overall, this study suggests that ant-guards in this system are effective against herbivory by three mega-herbivores and how different species of ants can vary in their effectiveness as ant-guards.

The patterns observed and documented here build on other studies that have demonstrated differences in tending by different plant-ant partners (Agrawal & Rutter, 1998; Rico-gray & Oliveira, 2007) and on other lines of evidence that have been gathered to document the effectiveness of ant species inhabiting *A. drepanolobium* (Young, Stubblefield & Isbell, 1997; Palmer & Brody, 2007).

This difference in tending/guarding suggests that differences in behaviour may be a key force driving the overall mosaic of ant-occupancy in this system. An example of the differences in behaviour towards the host acacia having serious effects has been documented in northern Kenya (Stanton *et al.*, 1999) where *C. nigriceps* prunes host acacias, thereby limiting plant reproduction. Pruning by *C. nigriceps* occurs in Kajiado, but approximately 25% of *C. nigriceps*-occupied trees at this site can be found with viable seed pods, suggesting that this behaviour may vary between populations (D. J. Martins, unpublished data). Pruning is relevant to herbivory as it results in higher numbers of more dense leafy shoots, which may be more attractive to herbivores (D. J. Martins, unpublished data; Stanton *et al.*, 1999). This study found the *C. nigriceps* was variable in its response to herbivores. This suggests that in addition to the pruning, this ant does not always behave as a mutualist towards its host tree when the tree is under attack by herbivores.

These antagonistic behaviours (pruning and not defending) may have impacts on the ants too. Antagonistic behaviour may reflect a wider pattern where ants attempt to maximize gains and reduce costs within the ant–plant partnership, as might be expected from simple models of inter-specific cooperation (Sachs *et al.*, 2004). However, this pruning results in higher number of leafy shoots and may explain why these trees with *C. nigriceps* are browsed despite their aggressive nature at the Suyian site, as browsing is also related to the leaf-thorn ratio (Estes, 1991; Madden & Young, 1992; Shorrocks, 2007). Browsing mammals may choose trade-offs of higher leaf-ratios over the irritation caused by the ants. Therefore, the pruning may both help and hinder the *C. nigriceps* colonies, and this interaction needs to be investigated further in relation to browsers.

The ability of workers of *C. mimosae* to perform as an ant-guard against all three herbivores suggests that foraging patterns and recruitment are key to the success of an

ant-guard in reducing herbivory. As both of these may be influenced by colony size as well as intrinsic differences between ant species (Fonseca, 1999; Barthlott, 2000), there is a need for further work in this system with other herbivore species. Small herbivores such as phytophagous insects need to be detected and repulsed evenly through time, while attacks by larger herbivores rely on rapid recruitment of nest-mates by ants. The ability of herbivores to recognize and avoid ant-acacias with particular ant species may have wider implications for host-tree success and account in part for why (through selective browsing) many African ant-acacias form near mono-dominant stands of trees with uniform architecture over large areas (Young, Stubblefield & Isbell, 1997; Palmer & Brody, 2007). In conclusion, this study highlights the importance of understanding the specifics of ant behaviour in ant–plant mutualisms as they are tested in the face of external pressures such as those exerted by browsing herbivores.

Acknowledgements

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