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Ant–plant conflicts and a novel case of castration parasitism in a myrmecophyte

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ABSTRACT

Questions: Do protective plant-ants perturb the pollination process and the reproduction of their host-plant? If they do, have partner selective mechanisms evolved against such conflicts?

Organisms: The semi-myrmecophyte *Humboldtia brunonis* and its ant associates.

Field site: Makut Reserve Forest, Western Ghats, South India.

Methods: We tracked insect and extrafloral nectar activity on inflorescences of several trees over a 24 h cycle. We repeatedly measured the extrafloral nectar produced by bracts of flowers throughout their phenology from the bud stage until and beyond flower opening. We studied the behaviour of ants towards the reproductive apparatus of the flowers and conducted ant exclusion experiments to test for any negative effect on herbivores or fruit production.

Conclusions: Pollinators did not visit inflorescences that had more than four ants on them. Ants, solely by their presence on bud bracts and bracteoles, intimidate other insects, both pollinators and herbivores. Some spatial and temporal mechanisms partially prevent negative ant–pollinator interactions. First, extrafloral nectar production on the bracts of flower buds, which attracts ants to inflorescences, was highest at night, attracting the largest numbers of ants at that time, whereas the major pollinators were active during the day. Second, this extrafloral nectar production declines after the first flower of each inflorescence opens. Third, the anthers and stigma are placed at the apex of a thin elongate axis, which offers a precarious foothold to ants. One ant species, *Crematogaster dohrni*, succeeds despite these difficulties by acting just before the flower opens, and damaging the flower when the style and stamens are still folded. This is the fourth case of castration behaviour of a plant-ant directed against its host-plant. Despite its anti-herbivore protection of flower buds, this plant-ant has a negative impact on fruit production in *H. brunonis*.

Keywords: ant–plant interactions, ant–pollinator conflict, castration parasitism, *Crematogaster dohrni*, defence–pollination conflict, extrafloral nectar, *Humboldtia brunonis*, myrmecophyte, partner selective mechanisms.

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INTRODUCTION

Many plants invest resources in defending their flowers against ants because ants are usually ineffective pollinators (Hölldobler and Wilson, 1990), potential enemies of pollinators (McDade and Kinsman, 1980; Willmer and Stone, 1997), may chemically inhibit pollen germination (Beattie *et al.*, 1984), may reduce pollen viability (Wagner, 2000), or may be floral nectar thieves (Guerrant and Fiedler, 1981; Haber *et al.*, 1981; Galen, 1999). Myrmecophytes, which are involved in symbiotic relationships with ants, are therefore especially concerned with potential conflicts with ants for their reproduction (Ghazoul, 2001). Most myrmecophytic symbioses are mutualisms, in which the plants provide ants with food and nesting structures called domatia and the ants protect them against herbivores or against competing vegetation, or provide them with nutrients (Davidson and McKey, 1993; Heil and McKey, 2003). However, conflicts exist in such mutualisms (Gaume *et al.*, 1998; Gaume and McKey, 2002; Izzo and Vasconcelos, 2002), as in others (Herre *et al.*, 1999), and some plant-ants are even parasites of myrmecophytes (Janzen, 1975; Gaume and McKey, 1999; Yu, 2001). Because the more the plant invests in growth, the more it invests in resources for ants such as nesting structures and extrafloral nectar (McKey *et al.*, 1999), selection on ants might favour mechanisms that increase the plant's allocation to growth at the expense of its allocation to reproduction. This is perhaps why some plant-ants have evolved a plant-castrating behaviour (Yu and Pierce, 1998; Stanton *et al.*, 1999; Izzo and Vasconcelos, 2002; Ute Moog, personal communication), in which the ants damage flowers and thereby affect the reproduction of their host-plant.

While ant–pollinator conflicts or direct ant–plant conflicts have rarely been documented in mutualistic ant–plant systems, this is partly because they were rarely looked for. Furthermore, strong selective pressures have probably led to their avoidance. In such symbiotic systems, partner selective mechanisms have often evolved that promote fidelity, prevent cheaters or retaliate against them (Bull and Rice, 1991; Ghazoul, 2001). There might be, for example, temporal or spatial separation of the activity of ants and pollinators (Raine *et al.*, 2002). In *Hirtella myrmecophila*, domatia abortion in old branches where flowering occurs is suggested to be a plant strategy to offset the negative effects of castration by the ant *Allomerus octoarticulatus* (Izzo and Vasconcelos, 2002). The extrafloral nectaries of some plants might distract ants from visiting flowers (Wagner and Kay, 2002). Moreover, many plants (Feinsinger and Swarm, 1978; Guerrant and Fiedler, 1981; Harley, 1991; Prŷs-Jones and Willmer, 1992; Galen and Cuba, 2001), including myrmecophytes (Willmer and Stone, 1997; Ghazoul, 2001; Raine *et al.*, 2002), have evolved chemical or physical devices against ants on their flowers.

Humboldtia brunonis (Fabaceae: Caesalpinioideae) is a semi-myrmecophyte, in which trees bearing domatia and those without domatia co-occur in the same population. This non- specialized ant-plant is, therefore, an appropriate model to show both the existence of such ant–plant conflicts for reproduction and the selective pressures acting on partner selective mechanisms. We therefore investigate such ecological conflicts in this non-specialized ant-plant and report a new case of castration behaviour of a plant-ant directed against its host-plant.

We first asked the following questions:

1. Do ants patrol flower buds and inflorescences? If they do, which species are patrollers and what are their behaviours towards the pollinators and the reproductive apparatus of the plant?
2. How do activity patterns of ants and pollinators vary over the 24 h cycle?

3. What is the temporal pattern of production of extrafloral nectar by bracts over the phenology of the inflorescence? Is it correlated with ant activity?

We then investigated the plant-castrating behaviour and asked:

4. How has the ant managed to counter the protective ant barriers erected by the plant?
5. Does this parasitic behaviour have an effect on plant reproductive success?
6. Is castration a cheating behaviour that results from strong selective pressures, or does it reflect some older life-history traits of the ants that are no longer adaptive?

MATERIALS AND METHODS

Study species

Humboldtia brunonis Wall. (Fabaceae: Caesalpinioideae) is an endemic semi-myrmecophytic understorey tree (up to 14 m tall) of the southern Western Ghats of India (Ramesh and Pascal, 1997). It belongs to a complex of six species of the genus *Humboldtia* (Sanjappa, 1986). Compared with *H. laurifolia*, which is a true myrmecophyte (Krombein *et al.*, 1999), *H. brunonis* is polymorphic for the presence of caulinary domatia, which are swollen internodes. In the same population, some trees possess domatia, while others do not. A large diversity of microfauna, including a number of ant species, inhabits the domatia of *H. brunonis* (Rickson *et al.*, 2003). The inhabiting ant colonies feed on extrafloral nectaries on leaves, stipules and flower bracts of all plants. We conducted the research between March and April 1999 in Makut Reserve Forest, Coorg District, Karnataka State (latitude: 12°05′N, longitude: 75°44′E). The two main ant species found in the domatia were *Crematogaster dohrni* Mayr (Myrmicinae) and the nomadic *Technomyrmex albipes* Smith (Dolichoderinae) ($n = 273$ domatia from 106 domatia-bearing trees). Although *C. dohrni* is not exclusively a domatia inhabitant, in this study site at the time of the observations it appeared to nest mainly in *H. brunonis* domatia. By contrast, *T. albipes* was also found to construct carton nests on *H. brunonis* trees and neighbouring plants. The flowering period is between December and April. We studied 104 trees that flowered in sunny habitats, 42 trees with domatia and 62 without.

Effect of time of day on extrafloral nectar production by floral buds and insect activity on inflorescences

In addition to young leaves, bracts and bracteoles on inflorescence buds (inflorescences whose flowers are still in the bud stage) produce a large amount of extrafloral nectar. Rhythms of this extrafloral nectar production and of insect activity on inflorescence buds were studied concurrently during a 24 h period commencing at 11.00 h.

On each of seven randomly chosen trees, we applied Tanglefoot glue at the base of one fully developed inflorescence bud to exclude ants, and wiped the nectar droplets off, every 2 h, after counting the total number of extrafloral nectar droplets that were produced. On these seven trees, plus another five randomly chosen ones, we selected two partially opened inflorescences (except for three trees where only one inflorescence was chosen) on which we recorded the number of insects, every 2 h, assigning them to the following categories: patrolling ants, pollinators or herbivorous insects. *Humboldtia brunonis* is outcrossed, pollinated mostly during the day, largely by small bees such as the allodapine *Braunsapis* (M. Shenoy and R.M. Borges, in prep.). In the present study, insects that were assigned to 'pollinators' were observed to contact both anthers and stigmas and to fly between flowers.

We conducted repeated-measures analyses of variance (using SAS GLM procedures), wherein repetitions were the 12 records of the 24 h period, in order to examine the effect of time on (1) bud extrafloral nectar production, (2) insect and (3) ant activity on opening inflorescences. The effects of other factors, such as tree ($n = 12$) and insect category ($n = 3$), were also examined in analysis (2), and the effect of ant species ($n = 5$) in analysis (3).

Effects of calendar day and floral phenology on extrafloral nectar production and insect activity on inflorescences

On each of 10 trees followed daily in the same order from 9 to 24 March 1999, we chose two small inflorescence buds ~2.5 cm long, one for extrafloral nectar production, the other for ant activity. We wiped off nectar on the inflorescence bud followed for extrafloral nectar production and enclosed it in a mesh bag to prevent nectar collection by insect visitors. Each morning (07.00 to 08.00 h), the total nectar produced per inflorescence was measured using 1 μl microcapillary tubes. On the inflorescence bud chosen for ant activity, we punctually recorded the total number of insect individuals and species three times a day (morning, noon and evening). We also measured the length of inflorescence buds every 2 days and noted their phenological stage daily (especially bud colour and first flower opening). Three of the extrafloral nectar inflorescence buds were disturbed by monkeys and one of the insect activity inflorescence buds was damaged by herbivory. Thus, only seven inflorescence buds were available for extrafloral nectar production analyses and nine for insect activity analyses.

We conducted a repeated-measures analysis of variance (ANOVA) to test for the effect of calendar day on extrafloral nectar production, followed by a three-factor ANOVA with repeated measures on two factors to test for the effect of insect category (ants versus others), calendar day and period of day (morning, noon, evening) on insect numbers on inflorescence buds.

To analyse the effect of inflorescence phenology, for each inflorescence we noted the opening day of the first flower (day d) and accordingly arranged data in the order of d to $d-1$, $d-2$ . . . and d to $d+1$, $d+2$ . . . As inflorescence buds did not begin to flower on the same date, analyses were done on a data set that covered the maximal duration for which no missing values were obtained taking all inflorescences into consideration. This covered a 13 day ($d-6$ to $d+6$) period. As the period of day did not significantly affect insect activity in the previous analysis, we pooled the data for the three periods and obtained a mean number of insects per day. We then performed a new repeated-measures ANOVA to test for the effect of phenological stage on extrafloral nectar production of inflorescences. We also compared insect numbers on inflorescences along their phenological stage for different categories (ants versus others) and for different ant species.

Effect of *Crematogaster dohrni* on fruit production

On the 104 trees studied for flower activity, we measured the height of the tree, recorded the ant species that patrolled the flowers during the entire study, and counted the total number of fruits present at the end of the study period. Trees that were patrolled by *Crematogaster* *dohrni* ($n = 43$) were mostly patrolled by this species (but not always exclusively), and the other trees ($n = 61$) were patrolled by several other opportunistic ants or exclusively by *Technomyrmex albipes*. Using *t*-tests, we compared the total fruit production, corrected for tree size, between these two samples of trees. Any negative effect of *C. dohrni* on the reproductive output of its host-plant could result from either its castrating behaviour or from its inefficient anti-herbivore protection. To distinguish between these two possibilities, we carried out an ant-exclusion experiment on inflorescence buds of 15 *Crematogaster*-patrolled trees. We chose 25 pairs of inflorescence buds of comparable size (about 2.5 cm long) on 25 branches belonging to 15 trees. For each pair, one inflorescence bud was left intact with *Crematogaster*-patrolling workers, while ants were excluded from the other by Tanglefoot. After 7 days, we recorded the number of herbivorous insects on both ant-patrolled and ant-excluded inflorescences of the 25 pairs. Eighteen days later, we recorded the number of fruits produced on each inflorescence bud. We then compared ant-patrolled and ant-free inflorescences for herbivore number and fruit number, using Wilcoxon's test for paired samples. This paired design enabled us to factor out uncontrolled variations among branches in terms of ant patrolling intensity and resource availability.

RESULTS

Identity and behaviour of ants and other insects visiting inflorescences

Seventeen ant species (Table 1) were attracted by the extrafloral nectar of the inflorescence buds (Fig. 1c) of *H. brunonis*. Among them, seven nested within domatia, as did the two

Table 1. Ant species patrolling the flower buds of *Humboldtia brunonis* ($n = 104$ trees)

Subfamily	Species	Number of trees
Dolichoderinae	***Tapinoma melanocephalum***	4
	Tapinoma sp.	7
	Technomyrmex albipes	35
Formicinae	***Camponotus angusticollis****	5
	Camponotus confucii	20
	*Camponotus infuscus**	4
	Camponotus near *varians**	1
	Oecophylla smaragdina	1
	Polyrhachis exercita	2
	Polyrhachis illaudata	2
	Polyrhachis sp.	1
Myrmicinae	***Cataulacus taprobanae***	10
	Crematogaster dohrni	43
	Crematogaster wroughtonii	3
	Monomorium monomorium	7
	Myrmicaria brunnea	1
Pseudomyrmecinae	*Tetraponera rufonigra**	1

Note: Species in **bold** face are those that also inhabit the domatia. *Exclusively nocturnal species.

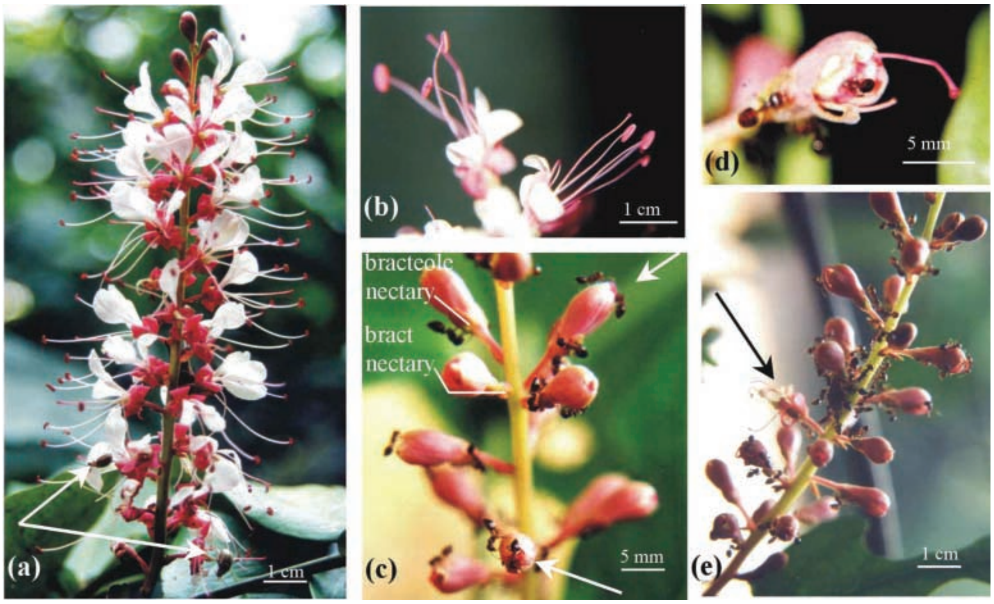


Fig. 1. Inflorescences of *Humboldtia brunonis* and the castration behaviour of *Crematogaster dohrni*. (a) An acropetalous flowering inflorescence. Note the absence of ants on opened flowers and the presence of two individuals of *Monolepta* sp. (Chrysomelidae) chewing on petals (arrows). (b) Opening flowers with thin elongated styles and anthers. (c) One or two days before the opening of the flower, *C. dohrni* workers are very numerous on the extrafloral nectar of bracts and bracteoles. They seem to be attracted by something inside the buds (arrows). (d) *C. dohrni* workers chew the protective sepals to obtain entrance to the bud and have pulled out style and stamens. (e) Ants are recruited *en masse* on the 'forced-to-open' buds. The arrow shows a 'castrated' flower with non-functional style and stamens.

most frequent species: *Crematogaster dohrni* and *Technomyrmex albipes*. Only *T. albipes* competitively excluded all other ants from inflorescences of plants it occupied. Extrafloral nectar visitors other than ants included wasps, flies and spiders. Except for two species, ants were never seen on the reproductive apparatus of the flower. The styles and stamens of the flowers are thin elongated poles, which have a whip-like motion and present precarious footholds for crawling visitors (Fig. 1a,b). Only *Tapinoma melanocephalum*, because of its very small size, was sporadically found walking 'safely' on the stamens without bending the filaments and falling. Another ant, *C. dohrni*, despite its larger size, also succeeded in contacting style and stamens, by acting before the flowers opened and exhibiting a castrating behaviour. Once the flower buds were fully elongated and acquired a dark pink colour, one or two workers of this species walked on a closed bud and began to pull out the protective sepals and/or chewed them to gain entrance to the bud (Fig. 1c). Then, with the abdomen often cocked upwards, they aggressively pulled out styles and stamens and injured them (Fig. 1d,e). At this point, the anthers had not yet dehisced. This behaviour was then followed by several other *Crematogaster* workers, which recruited in large numbers to the injured flowers (Fig. 1e). None of the ants was seen to collect floral nectar during these activities. This behaviour, despite some variation between colonies, has been observed in detail on at least 15 plants.

Ants in general did not collect floral nectar, which was produced in small quantities (mean = 0.88 μl per inflorescence, standard deviation = 0.83, $n = 4$ bagged inflorescences) and by very few flowers (1–4 per inflorescence) on few trees ($n = 4$ trees out of 8 in this quantification, but floral nectar was found to be absent from many other trees during visual inspections).

We recorded as putative pollinators (designated by observing body contact to anthers and stigmas) several generalist insects that were active during the day, such as social bees of the genera *Trigona* (Apidae, Apinae, Meliponini) and *Braunsapis* (Apidae, Xylocopinae, Allodapini, a species found nesting in the plant's domatia), and to a lesser extent solitary bees of the genus *Nomada* (Apidae, Nomadinae, Nomadini). Bees were recorded on 26 trees, of which *Trigona* spp. accounted for 15. Two species of beetles, including an undetermined curculionid species (three trees) and a buzzing *Plagiodera* chrysomelid (two trees), were seen touching anthers only during the daytime. There was never direct contact between ants and such probable pollinators because the thin elongated styles and stamens spatially separated them. While we did not observe any other pollinator during our several crepuscular observation periods and our 24 h observation session, subsequent experimental studies also suggest that nocturnal pollination is less important than diurnal pollination (M. Shenoy and R.M. Borges, in prep.).

A variety of herbivorous insects damaged inflorescences. Apart from a few homopterans (Coccidae, Membracidae and Flattidae), these were essentially chewing insects, which caused most damage once the flowers opened. Moth larvae were recorded on closed buds (Noctuidae and Geometridae) and opened flowers (Zygaenidae). Coleoptera (chrysomelids of the genera *Monolepta* [see Fig. 1a] and *Plagiodera* and a scarabid of the genus *Anomala*) were found mostly on flowers. Tettigoniids and phasmids severely damaged flowers only at night. The ants were rarely seen to behave aggressively towards herbivorous insects except against caterpillars, which they attacked, killed and ate (especially *C. dohrni* and *T. albipes*).

Activity of ants and other insects on inflorescences over a 24 h cycle

Ant patrolling activity over the 24 h cycle on partially opened inflorescences strongly depended on the ant species (Table 2a, Fig. 2a). *Technomyrmex albipes* deployed the largest number of workers, followed by *C. dohrni*, while the activity of other species was much lower. Activity patterns varied among ant species during the 24 h cycle (significant time × ant interaction; Table 2a). Some species were essentially nocturnal, whereas others were diurnal or were continuously active (Fig. 2a).

The number of insect visits on partially opened inflorescences was clearly dependent on the time of the day, and activity rhythms differed for different insects (Table 2b, Fig. 2b). Over the 24 h cycle, the mean number of ants on such opening inflorescences was significantly greater than that of herbivores and pollinators, which remained low. The mean ant activity was maximal between 19.00 and 21.00 h. Time, however, did not affect the abundance of the three categories of insects (ants, pollinators, herbivores) in the same way (significant time × insect interaction; Table 2b). For example, the pollinators were present only during the daytime (09.00 to 19.00 h), which was the period of least ant activity (Fig. 2b). However, during this period, there was a threshold number of ants (4 ants), beyond which the pollinator activity on the inflorescence dropped to zero (Fig. 3a). Moreover, the temporal abundance patterns of a major ant associate, *C. dohrni*, and of the pollinators were negatively correlated (Fig. 3b).

Table 2. Repeated-measures analyses of variance wherein the repetitions are the 12 records (every 2 h) of a 24 h cycle: (a) effects of time and ant species on number of ants on opening inflorescences; (b) effects of time and insect category (ant, pollinator, herbivore) on number of insects on opening inflorescences; (c) effect of time on extrafloral nectar production on inflorescence buds

(a) Number of ants on partially open inflorescences

Factor	d.f.	MS	*F*	*P*	*G-G*
Species	4	6097.26	44.30	0.0001	
Error	31	137.65			
Time	11	33.75	3.24	0.0003	0.03
Time × Species	44	37.54	3.60	0.0001	0.0005
Error (Time)	341	10.42			

(b) Number of insects on partially open inflorescences

Factor	d.f.	MS	*F*	*P*	*G-G*
Tree	11	760.28	125.65	0.0001	
Insect	2	5614.73	927.91	0.0001	
Insect × Tree	22	774.15	127.94	0.0001	
Error	27	6.05			
Time	11	22.14	16.73	0.0001	0.0001
Time × Tree	121	11.61	8.77	0.0001	0.0001
Time × Insect	22	22.35	16.89	0.0001	0.0001
Time × Insect × Tree	242	11.43	8.64	0.0001	0.0001
Error (Time)	297	1.32			

(c) Number of extrafloral nectar droplets produced by inflorescence buds

Factor	d.f.	MS	*F*	*P*	*G-G*
Time	11	249.90	3.26	0.001	0.05
Error	66	76.63			

Note: Probabilities corrected for sphericity are provided using the Greenhouse-Geiser correction (*G-G*).

The extrafloral nectar production of closed inflorescence buds was dependent on time of day (Table 2c) and reached a peak between 19.00 and 21.00 h (Fig. 2b), as did ant activity on partially opened inflorescences.

Influence of floral phenology on extrafloral nectar production and ant patrolling activity

The flower buds began to open only when the inflorescences reached their maximal size. Flowering was acropetalous (from base to apex of the inflorescence) and lasted 3–4 days. Flowers opened between 15.00 and 17.00 h. Style and stamens emerged in indeterminate order. Stamen dehiscence occurred at night, beginning near 19.00 h, and pollen was available in the anthers over 24 h. The stigma continued to be receptive the next day (M. Shenoy and R.M. Borges, in prep.).

While the calendar day did not affect the nectar production of bracts and bracteoles ($F_{15,90} = 0.27$, $P = 0.99$), there was a significant effect of the phenological stage of the

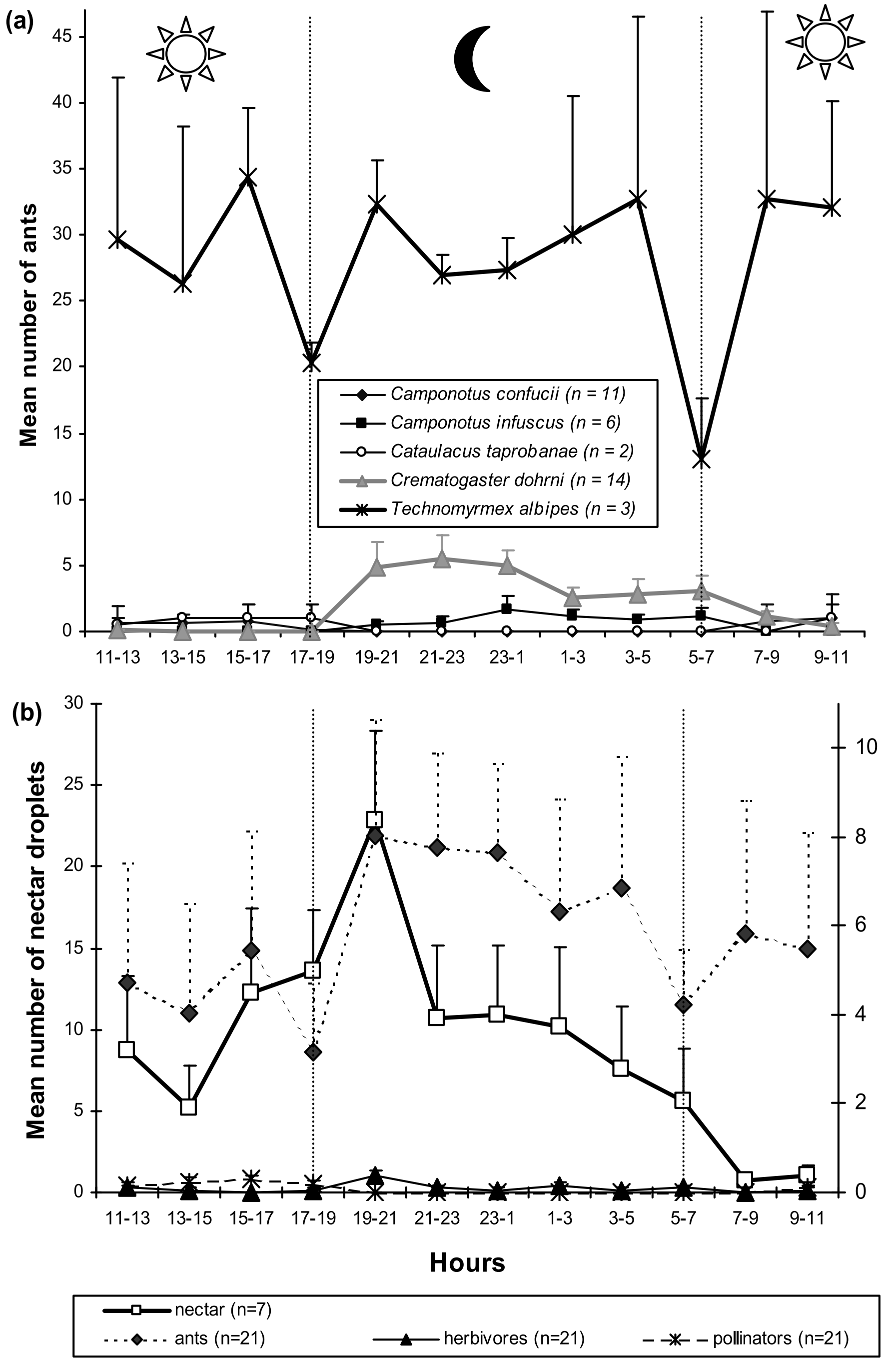
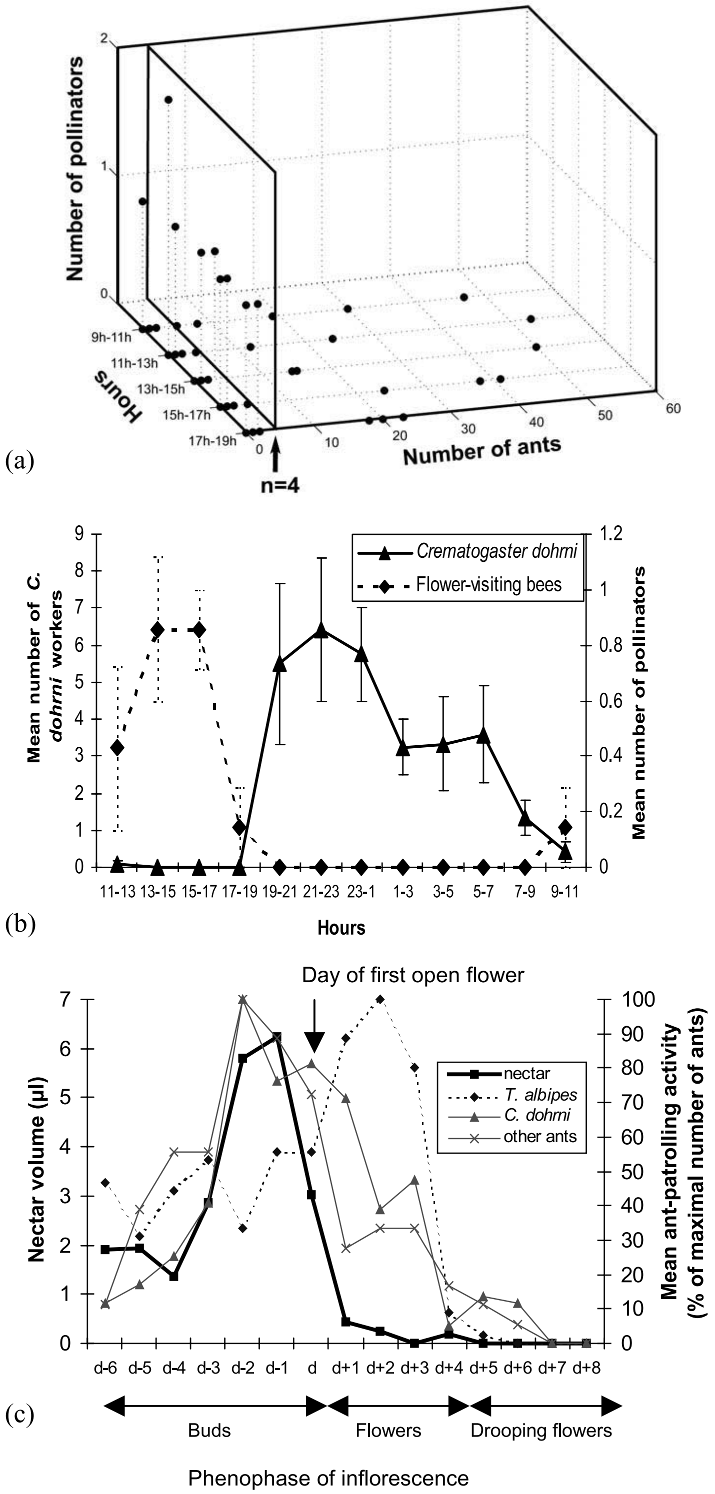


Fig. 2. Mean (± standard error) activity rhythms over the 24 h cycle on inflorescences. (a) Activity of different ant species. (b) Activity of extrafloral nectar production (*n* = 7 closed inflorescence buds) and of different insect guildes (*n* = 21 partially opened inflorescences).


(a)
Number of pollinators
0
1
2
Hours
9h-11h
11h-13h
13h-15h
15h-17h
17h-19h
Number of ants
0
10
20
30
40
50
60
n=4
(b)
Mean number of C. dohrni workers
0
1
2
3
4
5
6
7
8
9
Mean number of pollinators
0
0.2
0.4
0.6
0.8
1
1.2
Crematogaster dohrni
Flower-visiting bees
11-13
13-15
15-17
17-19
19-21
21-23
23-1
1-3
3-5
5-7
7-9
9-11
Hours
(c)
Day of first open flower
Nectar volume (µl)
0
1
2
3
4
5
6
7
Mean ant-patrolling activity (% of maximal number of ants)
0
10
20
30
40
50
60
70
80
90
100
nectar
T. albipes
C. dohrni
other ants
d-6
d-5
d-4
d-3
d-2
d-1
d
d+1
d+2
d+3
d+4
d+5
d+6
d+7
d+8
Buds
Flowers
Drooping flowers
Phenophase of inflorescence

inflorescence ($F_{12,72} = 2.53$, $P = 0.008$). Extrafloral nectar production increased until the day before the opening of the first flower (day *d*), then declined abruptly (Fig. 3c).

The phenological stage of the inflorescences explained the variability in the number of insect visits (Table 3b) more than the calendar day or the period of the day (morning, noon, evening; Table 3a), which did not appear to contribute significantly to the variance. In general, ants were significantly more numerous than other insects on the inflorescences (Table 3b; insect category significant), but detailed univariate procedures showed that this was true only for the 3 days preceding and including the opening of the first flower, which corresponded to the period of maximal extrafloral nectar production.

Inflorescence phenology had a strong effect on the number of ant visits, which also depended strongly on ant species (Table 3c). The means ± standard deviation of the 13 phenological means (from $d - 6$ to $d + 6$) of the number of patrolling ants per inflorescence bud (n = trees × 13 phenological stages) were, in decreasing order: 9.9 ± 6.2 for *T. albipes* ($n = 26$), 2.7 ± 1.9 for *C. dohrni* ($n = 52$), 0.2 ± 0.1 for *Camponotus confucii* ($n = 52$), 0.2 ± 0.2 for *Monomorium minutum* ($n = 52$), 0.16 ± 0.25 for *Tapinoma indicum* ($n = 39$) and 0.05 ± 0.10 for *Tapinoma melanocephalum* ($n = 26$). There was a trend for all the ant species to increase their activity up to 1–2 days before the opening of the first flower, tracking the pattern of nectar production (Fig. 3c). After this, activity varied for different ant species (significant ant × phenology interaction; Table 3c). Patrolling activity in most species began to decrease after the flowers opened, but this decrease was delayed for *C. dohrni* and was not observed for *T. albipes*, whose activity remained at a high level throughout the life of the inflorescences (Fig. 3c) as well as during fruit development (unpublished results).

Each insect species visiting the inflorescences concentrated its activity on a specific phenological stage. Wasps, flies and caterpillars were essentially active before the first day of flowering, while bees and beetles were active during the flowering process.

Effect of *Crematogaster dohrni* on herbivores and fruit production

Trees whose flowers were patrolled by *C. dohrni* ($n = 43$) produced 3.7 ± 5.8 fruits, whereas the other trees ($n = 61$) produced 7.3 ± 1.4 fruits. Trees patrolled by *C. dohrni*, therefore, produced significantly less fruits than the other trees [$t = -2.02$, $P = 0.045$ for unequal variances ($F_{60,42} = 4.14$, $P = 0.0001$)]. This difference cannot be attributed to non-homogeneous tree sizes between the two samples for the following reasons. First, mean tree heights of the two samples were not significantly different (mean = 6.0 m, standard

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Fig. 3. Ant–pollinator conflict and evidence for partner selective mechanisms. (a) Number of pollinators as a negative function of number of ants (all species included) on *H. brunonis* inflorescences over the five diurnal observation periods corresponding to pollinator activity. Each point refers to a partially opened inflorescence. (b) Temporal segregation between mean (± standard error) activity of the ant *C. dohrni* and the pollinating bees on *H. brunonis* opening inflorescences ($n = 14$). (c) Mean volume of extrafloral nectar produced per inflorescence ($n = 7$) and mean ant-patrolling activity over the developmental stage of the inflorescence (*T. albipes*, $n = 2$; *C. dohrni*, $n = 4$; others, $n = 13$). The amount of extrafloral nectar increases until the day before the opening of the first flower (*d*), then begins to drop. Mean ant-patrolling activity is expressed as a percentage of the maximum number of ants on inflorescence buds to permit comparisons of trends between species.

Table 3. Repeated-measures analyses of variance: (a) effects of insect category (ants *vs* others), calendar day ($n = 14$) and period of the day (morning, noon, evening) on number of insect visits on inflorescences of *H. brunonis*; (b) effects of insect category and inflorescence phenology ($n = 13$) on number of insect visits; (c) effect of ant species ($n = 6$) and inflorescence phenology on number of ant visits

Number of insects on inflorescences						
	Factor	d.f.	MS	*F*	*P*	*G-G*
(a)	Insect	1	247.58	3.84	0.06	
	Error	19	64.50			
	Calendar day	13	2.65	0.51	0.91	0.55
	Calendar day × Insect	13	3.61	0.70	0.77	0.47
	Error (Day)	247	5.18			
	Period	2	4.80	2.13	0.13	0.15
	Period × Insect	2	6.03	2.68	0.08	0.10
	Error (Period)	38	2.25			
	Day × Period	26	0.41	0.80	0.74	0.54
	Day × Period × Insect	26	0.33	0.65	0.90	0.65
	Error (Day × Period)	494	0.51			
(b)	Insect	1	170.18	4.39	0.05	
	Error	18	38.80			
	Phenology	12	6.10	2.96	0.0008	0.06
	Phenology × Insect	12	5.37	2.60	0.003	0.08
	Error (Phenology)	216	2.06			
Number of ants on inflorescences						
	Factor	d.f.	MS	*F*	*P*	*G-G*
(c)	Species	5	136.72	8.79	0.001	
	Error	11	15.55			
	Phenology	12	14.50	13.10	0.0001	0.001
	Phenology × Species	60	5.83	5.27	0.0001	0.003
	Error (Phenology)	132	1.11			

deviation = 2.8 m for *C. dohrni*-patrolled trees; mean = 6.4 m, standard deviation = 2.7 m for the others; $t = -0.73$, $P = 0.47$), while their variances were homogeneous ($F_{60,42} = 1.09$, $P = 0.75$). Secondly, the number of fruits/tree height was also significantly different between the two samples [mean = 0.5, standard deviation = 0.74 for *C. dohrni*-patrolled trees; mean = 1.0, standard deviation = 1.3 for the others; $t = -2.48$, $P = 0.01$ for unequal variances ($F_{60,42} = 3.13$, $P = 0.0001$)]. The difference in fruit production is mainly due to the fact that a greater proportion of *C. dohrni*-patrolled trees compared with the other trees produced no fruit at all (18 out of 43 trees versus 13 out of 61 trees: $\chi^2 = 5.09$, $P = 0.02$).

The ant-exclusion experiment showed that inflorescence buds with *C. dohrni* patrolling ants (control inflorescences) had significantly fewer herbivorous insects than those from which *C. dohrni* had been removed (Wilcoxon test for matched pairs: $n = 25$, $Z = 1.99$, $P = 0.047$) (Fig. 4a). The herbivorous insects were essentially microlepidopteran larvae and beetles of the genera *Monolepta* and *Anomala*. *Crematogaster dohrni* thus provides its

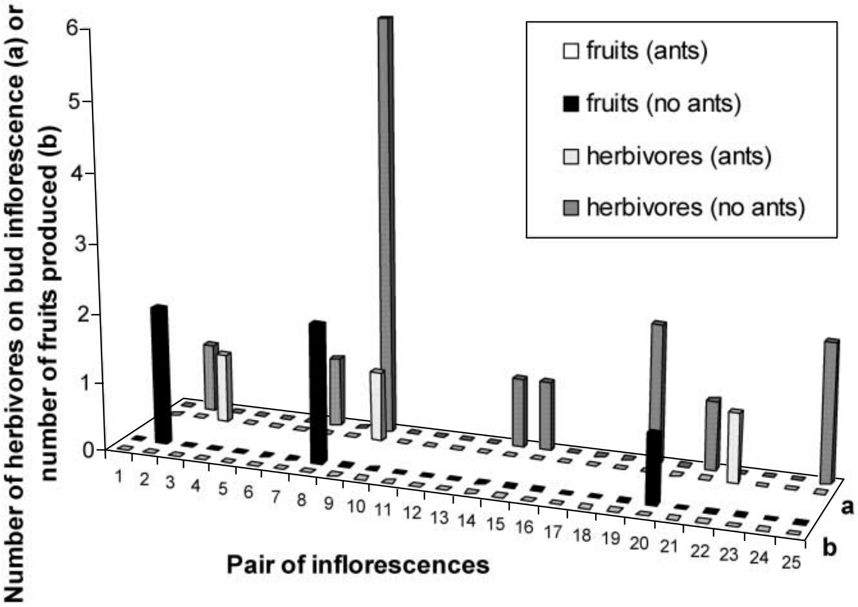

Fig. 4. Comparison between control (with ants) and experimental (ants excluded) inflorescence buds of (a) the number of herbivorous insects and (b) the number of fruits produced.

host-plant with some anti-herbivore protection. In this experiment, fruit production was globally very low. None of the 25 control inflorescences produced fruits and only three of the 25 experimental ones produced fruits (Wilcoxon test for matched pairs: $n = 25$, $Z = 1.6$, $P = 0.1$) (Fig. 4b). Thus, the only inflorescence buds that produced fruits were ones from which *C. dohrni* had been removed.

DISCUSSION

The results of this study clearly show that the non-specific and semi-myrmecophyte *Humboldtia brunonis* experiences direct and indirect conflicts for reproduction with its ant associates.

Conflict between ants and pollinators

Humboldtia brunonis attracts many ants to its inflorescences, just like some other plants that produce large amounts of extrafloral nectar on their flowers (Bentley, 1977; Inouye and Taylor, 1979; Schemske, 1980; Oliviera *et al.*, 1999). Although in many cases ants have been reported to enhance seed set by their anti-herbivore behaviour (Bentley, 1977; Rico-Gray and Thien, 1989; Del-Claro *et al.*, 1996; Willmer and Stone, 1997; Oliviera *et al.*, 1999), their presence on flowers may also decrease pollination success and seed set (Puterbaugh, 1998; Galen, 1999; Ghazoul, 2001). Few studies, however, have quantified the effects of ants on pollination success (but see McDade and Kinsman, 1980; Altshuler, 1999). One major reason for this lack of data may be that many flowering plants prevent ants from interacting directly with pollinators by chemical (Guerrant and Fiedler, 1981; Prŷs-Jones and Willmer, 1992; Ghazoul, 2001; Raine *et al.*, 2002) or physical (Feinsinger and Swarm, 1978; Juniper, 1995; Galen and

Cuba, 2001) means. Moreover, ant–pollinator conflicts might often remain cryptic because they are indirect (e.g. when ants solely by their presence, as in *H. brunonis*, deter visits by pollinators). These conflicts might partly explain why ant attendance sometimes does not have a positive effect on plant reproductive success (O'Dowd and Catchpole, 1983; Puterbaugh, 1998; Galen, 1999).

The deterrent effect of ants could also result in shorter durations of pollinator visits to flowers within a plant, thus promoting outcrossing between plants (Altshuler, 1999). This would therefore turn the conflict into an advantage for the plant. However, the resulting high proportion of cross-pollinating visits would probably be made at the expense of visit duration, thus affecting the amount of pollen exchanged. During our study period, fruit production in *H. brunonis* was low. We believe that the low number of pollinator visits to flowers and/or their brief visits caused by ant deterrence might partly explain this. High rates of fruit abortion caused by severe herbivore damage at the early stage of flowering might also contribute to low fruit production.

This study provides evidence for both spatial and temporal segregations of ants and pollinators on flowers. We suggest that partner selective mechanisms could have evolved in response to the plant's conflict between defence and pollination. The thin elongated styles and stamens of *H. brunonis* flowers spatially separate ants and pollinators. These filaments have a whip-like motion and might act as a mechanical barrier against ants or other crawling insects, which never venture onto them, except the very small ones. This trait, shared by several species of the Caesalpinioideae (Lewis *et al.*, 2000), might have nothing to do with ants. However, since mechanisms that can pre-empt potential ant–plant conflicts might be widespread in angiosperms (Ghazoul, 2001), we propose that this trait could belong to what has been coined the 'greasy pole syndrome', which dislodges crawling insects such as ants (Harley, 1991; Juniper, 1995). This trait could have simply been exaggerated in plants which have closer interactions with ants, such as the myrmecophyte *H. brunonis*. A good demonstration of how evolution of flower shape might be influenced by such ant–plant conflict was provided by Galen and Cuba (2001) and underlines the importance for structural partner selective mechanisms. Temporal mechanisms of segregation might also occur. The temporal separation between the diurnal pollinating bees and the nocturnal ant *C. dohrni* is possibly due to increased extrafloral nectar production at night. Extrafloral nectar could therefore play a substantial role in ant distraction (Wagner and Kay, 2002) during the pollination period. A second temporal segregation is mediated by the plant's floral phenology: one day before the first flower opens, the extrafloral nectar production of bracts and bracteoles on the inflorescence bud begins to fall. This abrupt decrease probably causes the decline in activity observed for most ant species on the inflorescences once flowering begins. This temporal pattern might simply reflect the shutdown of a costly resource such as nectar during the expensive phase of pollination and seed initiation. But it may also be an adaptive 'phenological barrier' similar to those reported in other ant–plant symbioses, where ants reduce their activity on flowers only during the period of anthesis, probably because of chemical repulsion by floral tissue (Willmer and Stone, 1997; Ute Moog, personal communication). However, this 'phenological barrier' is not effective against two main ant associates: *C. dohrni*, whose activity at the inflorescence continues until their 'castration' behaviour, and *T. albipes*, whose activity can remain high even after the flower opening phase.

Conflict between *Crematogaster dohrni* and its host-plant

The presumed partner selective mechanisms described above appear to be ineffective against *Crematogaster dohrni*, which by acting before the flowers open, bypasses any spatial and temporal barriers and exhibits a castrating behaviour. Like some other plant-ants (Janzen, 1975; Yu and Pierce, 1998; Gaume and McKey, 1999), this species behaves as a parasite of its host-plant, since it has been shown to have a negative impact on the plant's fitness at least during the study period. A thorough investigation during the whole period of plant reproduction needs to be undertaken to measure the extent of such a parasitism. The negative impact observed on fruit production is most likely the result of the castrating behaviour of *C. dohrni*, since the ants do provide some level of protection against phytophagous insects.

Since floral nectar is almost never harvested by *C. dohrni*, the castration behaviour is not the result of damage caused by nectar-foraging activities as in other ant–plant interactions (Galen, 1999). This, therefore, raises several questions. Is this species a 'cheater' in the sense of a species that enhances its fitness by exhibiting such a behaviour and not providing reciprocal benefits to its host-plant? (Yu, 2001; Izzo and Vasconcelos, 2002). Or does this behaviour originate from other causes, which are no longer adaptive?

First, could this castrating behaviour enhance the fitness of the ant? One evolutionary explanation was proposed by Yu and Pierce (1998). By decreasing the plant's allocation of resources to reproduction, castration may increase the plant's allocation to growth, resulting in provision of more resources for ants, such as domatia and extrafloral nectar. Enhanced growth rate of the host, consequent to castration parasitism, is frequent in other host–parasite systems (e.g. Baudoin, 1975; Sousa, 1983; Clay, 1990; Kover, 2000). A rigorous test of this hypothesis would require very long-term investigations for our slow-growing understorey tree. However, it is a plausible hypothesis for the *C. dohrni*–*H. brunonis* system, provided that there is a long-term relationship between the ant colonies and the plants. *Crematogaster dohrni* is not a true symbiotic species in the sense that it is not restricted to *H. brunonis* as a host-plant. However, it is a major ant associate of *H. brunonis*, and appears to be regularly associated with the plant (unpublished results from two consecutive years). Such fidelity provides the opportunity for ants to influence plant reproductive success (Horvitz and Schemske, 1984), and therefore their own reproductive success, as in true symbiotic systems. We thus cannot rule out the hypothesis that *C. dohrni* has developed castration behaviour as part of a selfish and 'cheating' strategy. Nevertheless, we suggest alternative explanations for this castration behaviour and will discuss their adaptive significance.

The castrating behaviour of *C. dohrni* might merely result from an ancestral pruning habit of arboricolous ants, wherein pruning of plant 'bridges', such as vines or young stems, may prevent competition with other ant colonies for their host-plant (Davidson *et al.*, 1988; Stanton *et al.*, 1999; Federle *et al.*, 2002; Palmer *et al.*, 2002). Pruning in the pan-tropical genus *Crematogaster* has so far been reported on *Macaranga* in Asia (Hölldobler and Wilson, 1990, p. 552; Federle *et al.*, 2002) and for the African *C. nigriceps* on *Acacia drepanolobium* (Stanton *et al.*, 1999). Competitive pressures may be the ultimate factors causing such behaviour. Recent studies on plant-ants have also shown that young vegetative tissue contains chemical compounds such as methyl salicylate to which ants are very sensitive (Brouat *et al.*, 2000). We suggest that some chemical constituents of the developing reproductive bud tissue might induce attraction and 'aggression' and constitute the proximate causes of the pruning and/or castrating behaviour of *C. dohrni*. Indeed, the behaviour of the ants that recruit *en masse* to flower buds and try to enter the buds suggests a reaction to volatile compounds emitted by the floral nectar or more probably by tissue inside the calyx. However, in *H. brunonis*, most of the ant species seem to be repelled from opening flowers, while only *C. dohrni* is obviously attracted and develops 'aggression'. Why? Ant-repelling compounds have probably been selected in flowers of ant-plants (Willmer and Stone, 1997; Ghazoul, 2001; Raine *et al.*, 2002) and might repel non-pruning ants. Another explanation would be that compounds similar to methyl salicylate emitted by many flowers during pollination (Knudsen and Tollsten, 1993) and known to mimic alarm pheromones of some ants (Duffield *et al.*, 1975) might repel most ants and elicit aggression only in a few dominant species. Interspecific variation in ant behaviour towards flower tissue has previously been reported where the few ants, including a *Crematogaster* species, that were not repelled by the floral tissue developed 'aggression' against it (Ghazoul, 2001).

CONCLUSION AND OUTLOOK

Several hypotheses have been proposed to explain the castrating behaviour developed by *C. dohrni* towards its host-plant. This behaviour might have been under active selection or a by-product of other selective forces. We plan to explore the chemical ecology of this ant–plant system to determine whether chemical signals of the opening buds elicit the castration behaviour. Whatever its origin, this behaviour seems to affect the plant's fitness. As *H. brunonis* is a semi-myrmecophyte, we wonder whether this *Humboldtia*–ant system will persist over evolutionary time. The parasitic ant might be maintained in the system if other domatia-inhabiting ants, such as *Technomyrmex albipes*, have counterbalancing effects on the plant's fitness (this will be the focus of another paper), or if in the co-evolutionary arms race, the plant evolves mechanisms that 'cheat the cheater'. Models of species co-existence based on a population approach would be helpful in understanding the evolutionary dynamics of such ant–plant systems.

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