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The interaction of thorns and symbiotic ants as an effective defence mechanism of swollen-thorn acacias

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Abstract Evidence is provided for the interaction of ants (*Crematogaster* spp.) and thorns as a means of defence against browsing mammals for one species of African myrmecophyte, *Acacia drepanolobium*. Two experiments were conducted using goats as representative mammalian browsers. In the first experiment, the defences of individual branches were manipulated in order to assess the effectiveness of ants and thorns both on their own and together as anti-herbivore defences. It was shown that ants on their own are more effective defences for a single branch than having neither ants nor thorns, but ants from a single branch do not add significantly to the effectiveness of thorns as an anti-herbivore defence. The second experiment looked at the effect of a whole tree of ants and how they interacted with thorns in the defence of the tree. It was shown that ants from a whole tree do significantly add to the effectiveness of thorns as an anti-herbivore defence. In all cases, the goat refused to go back to and feed from a tree whose ants had just attacked it. Thorns on their own, however, do not act as total browsing deterrents. They slow down the rate of feeding but animals may compensate for this by feeding for longer periods of time. The interaction of a whole tree of ants and thorns is a very effective browsing deterrent which causes the animal to stop feeding almost immediately, therefore keeping the amount of foliage lost to a minimum. These results provide support for the hypothesis that the ant-acacia relationship (in the case of *A. drepanolobium*) evolved at least partly because of pressure from browsing mammals.

Key words Thorns · Acacia ants · Defence · Mammals · Herbivory

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Introduction

Many plants possess naturally hollow structures that are used as shelter by a variety of insects. Only a few of these are true myrmecophytes in that they have a symbiotic relationship with ants, harbouring them in preformed cavities (domatia) and providing sources of food (Jolivert 1996). Bequaert (1922) quotes 262 myrmecophytic species in the world, whilst Benson (1983) quotes 465 species. The best-known examples are from the genus *Acacia* (Leguminosae; Mimosoideae) in South America (Belt 1874; Janzen 1966) and Africa (Monod and Schmitt 1968; Hocking 1970; Ross 1981), the so-called ant-acacias.

This study considers the interaction of symbiotic ants (*Crematogaster* spp.) and the thorns of an African ant-acacia, *Acacia drepanolobium* (Sjöstedt) as a means of defence against mammalian browsers. In this study, I investigated the relative effectiveness of each, and their combination, as a defence mechanism.

Whilst the effectiveness of symbiotic ants (Madden and Young 1992) and thorns (Young 1987) on their own as a means of defence of *A. drepanolobium* has been considered, the interaction of ants and thorns as a defensive measure has been ignored. The fact that the trees invest energy and resources in thorns as well as ants suggests that there is an important interaction between them which provides a more effective defence than either on its own.

The armature of long, sharp thorns is a characteristic of ant-acacias and some other *Acacia* species. However, in the ant-acacias, a number of these thorns are swollen at the base, and it is here that ants live and rear their brood. The unswollen thorns have an uncertain effect in defending the plant against mammalian browsers (Cole 1986; Potter and Kimmerer 1988; reviewed Myers and Bazely 1991). In *A. drepanolobium*, for example, intense browsing pressure from mammals induces an increase in both the density and number of longer thorns produced (Young 1987; Milewski et al. 1991), suggesting that thorns are important in defending the plant. In another *Acacia* species [*A. tortilis* (Forssk.) Hayne], however, an increase in the density of thorns protects the twigs but not necessarily the leaves of the plant from being browsed by goats (Gowda 1997). Cooper and Owen-Smith (1986) showed that thorns are effective in as much as they slow down the feeding rate of generalised browsing mammals (goat, lesser kudu, impala), but that the mammals compensate for this by feeding for a longer period of time. Thorns affect larger browsers less than small browsers. For example, Foster and Dagg (1972) and Pellew (1984) showed that the ingestion rate of giraffes (*Giraffa cameloparda*) is not affected by thorns of *A. drepanolobium*. Therefore, although thorns appear to be an inducible response to mammalian browsing pressure, their actual effectiveness as an anti-herbivore defence against specialised herbivores at least is not very clear.

Another characteristic of ant-acacias are the extra-floral nectary glands on the leaf petioles that provide the ants with nutrients (Knox et al. 1986). Some South American species of ant-acacias also produce proteinaceous beltian bodies that the ants harvest (Janzen 1966). These bodies are lacking in the African ant-acacias. The ants are known to defend the plant against fire (Janzen 1967b), encroaching vegetation (Janzen 1967a) and possibly browsing by mammals and insects (Janzen 1966; Hocking 1970; Knox et al. 1986; Schupp 1986; Madden and Young 1992). Interestingly, there are no ant-acacias in Australia despite the diversity of the acacia genus there, nor are there abundant browsing mammals similar to those seen in Africa or South America. Based on this observation, Brown (1960) argued that it was the role of ants as defences against browsing mammals that led to the evolution of the ant-acacia relationship and suggested that this is the main benefit that the plant receives from the interaction.

Materials and methods

The study site and species

I carried out the study during May–July and October–December 1996 in Mkomazi Game Reserve, northern Tanzania. The reserve is covered by *Acacia-Commiphora* bush land, with *A. drepanolobium* confined to areas of seasonally inundated black cotton soils. There is a biannual pattern of rainfall, with the long rains in April–June and the short, heavier rains in November–December.

A. drepanolobium is a small, many branched tree up to 3 m in height (in undisturbed areas it can reach 7 m high; Coe and Beentje 1991). The trees are characterised by an armature of long, sharp white thorns (up to 7.6 cm in length) with many swollen at the base (personal observation). When they are young, the swollen thorns are hollow, green and soft with the inside covered in pithy material and a petiole leaf attached to the midpoint of the gall face. As they age, the petiole leaf is lost, leaving behind a scar. The swollen thorns gradually darken and harden with age becoming red/brown and eventually black.

The swollen thorns on *A. drepanolobium* studied in Mkomazi are inhabited by colonies of *Crematogaster nigriceps* Emery (Formicidae, Myrmicinae). In other sites, up to four species of ant coexist and the ant species may vary according to tree height (Young et al. 1997). The ants are quick to respond to a disturbance, emitting an acrid smell and raising their abdomens above their heads. They are able to inflict a vicious bite which is exacerbated by rubbing acid into the wound (Hocking 1970; personal observation).

Methods

The study was divided into two experiments using a different goat in each. (It was not practical to use more than one goat in each part of the experiment; see Milewski et al. 1991). I conducted experiment 1 in the research camp, and in experiment 2, took the goat to the trees.

Experiment 1: how effective are ants and thorns both on their own and together as anti-herbivore defences?

I collected eight branches at random from an individual tree, each branch being approximately the same in terms of vegetation cover and swollen thorn number. I plugged the swollen thorns in the field using thorns to avoid loss of ants during transportation. At the research camp, I tagged branches and randomly allocated a defence condition to produce two branches of each condition. The defence conditions were: (3) thorns and ants (natural defence condition); (2) thorns only (swollen thorns kept plugged, stray ants picked off); (1) ants only (all thorns cut off using secateurs), and (0) no ants or thorns (thorns and ants removed or constrained within swollen thorns).

I weighed the branches and then offered them to the goat in a random order (approximately 30 min after the branches had been removed from the trees). The goat was allowed to feed for 30 s during which time I recorded the number of bites taken. A break of 1 min was allowed between each branch. Once all the branches had been offered, I reweighed them at the same time to avoid differential weight loss due to transpiration. I was then able to calculate the amount of vegetation eaten and average bite size (amount of vegetation eaten divided by the number of bites taken).

I repeated the experiment over a period of 5 days, for ten different trees, two trees being tested on each day.

Experiment 2: what is the effect of a whole tree of ants and/or thorns as an anti-herbivore defence?

I chose ten trees of similar size and vegetation cover from a study plot. I removed the resident ants from five of these trees by clearing vegetation from around the base of the tree, applying a ring of Hyvis to the trunk (to prevent ants from moving back onto the tree) and then hitting the tree repeatedly with a pole.

I took the goat to the plot and it was offered each of the trees in turn for feeding. The tree condition (ants versus no ants) was determined by the toss of a coin. The goat was allowed to feed for a maximum of 5 min, during which time I recorded the number of bites taken, the approximate percentage of available vegetation eaten (estimated by comparing the amount of foliage remaining on the tree to the amount of foliage present before the experiment began) and reaction to defences (e.g. shaking of head, scratching head with hooves, sneezing, stopping feeding). I repeated the experiment four times, each time on a different day.

Both experiments were carried out between 0730 and 1030 hours. In each case, I prevented the goat from eating during the previous night.

Statistical methods

I analysed the results for experiment 1 using a two-way ANOVA. The results for experiment 2 were analysed using a two-sample t-test and the Mann-Whitney U- test.

Results

Experiment 1

Amount of vegetation eaten varies according to branch defence

The presence of ants and thorns on a single branch (3) does not add significantly to the effectiveness of thorns or ants on their own as defensive measures with respect to the amount of vegetation consumed in 30 s (there was no significant interaction between ants and thorns: two-way $F_{1,76} = 1.66$, $P = 0.202$). Ants on their own (1) and thorns on their own (2) had a significant effect on the amount of vegetation consumed (two-way $F_{1,76} = 4.06$, $P = 0.048$, $F_{1,76} = 20.05$, $P < 0.0001$, respectively; Fig. 1). Therefore, significantly less vegetation is consumed from branches with ants (1) or thorns (2) than from branches lacking both defences (0). The amount of vegetation consumed from branches with both ants and thorns (3) is not significantly different compared with the amount consumed from branches with either ants (1) or thorns (2).

Number of bites taken varies according to branch defence

The presence of ants and thorns on a branch (3) adds significantly to the effectiveness of thorns (2) or ants (1) on their own as defensive measures with respect to the number of bites taken in 30 s (there was a significant interaction between ants and thorns: two-way $F_{1,76} = 6.00$, $P = 0.017$). Ants or thorns on their own had significant effects on the number of bites taken in 30 s (two-way $F_{1,76} = 12.62$, $P = 0.001$, $F_{1,76} = 113.55$, $P < 0.0001$, respectively; Fig.1). Therefore, with increasing defences, fewer bites are taken from a single branch.

Bite size is not affected by the type of branch defence

The presence of ants and thorns on a single branch (3) does not add significantly to the effectiveness of thorns or ants on their own as defensive measures with respect to bite size (there was no significant interaction between ants and thorns: two-way $F_{1,76} = 0.06$, $P = 0.804$). Neither ants nor thorns on their own had a significant effect on bite size (two-way $F_{1,76} = 0.34$, $P = 0.562$; $F_{1,76} = 0.00$, $P = 0.981$, respectively; Fig. 1). Therefore bite size is not affected by thorn and/or ant branch defences.

Experiment 2

Length of browsing time is reduced by the presence of ants

On each day, the goat took significantly more bites and ate significantly more of the available foliage from trees that were lacking ants than from trees inhabited by ants (Table 1).

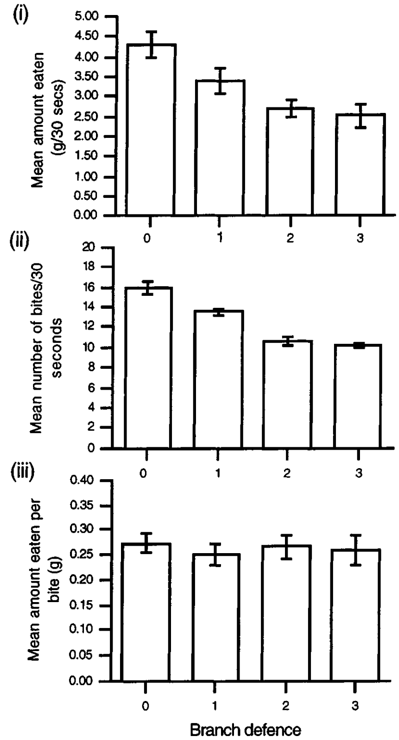

Fig. 1 Mean amount of vegetation eaten (g) in 30 s (*top*), mean number of bites taken in 30 s (*middle*) and mean bite size (g) (*bottom*). See text for statistical analysis (branch defence: *0* no ants, no thorns; *1* ants only; *2* thorns only; *3* ants and thorns). Error bars show the standard error of the mean

Table 1 The mean number of bites taken and the median amount of vegetation eaten (%) from trees inhabited by ants and from trees lacking ants. The sample size is five in each case. The hypothesis of no significant difference between the results for each tree type was tested with a two-sample *t*-test (number of bites) and Mann-Whitney *U*-test (% vegetation eaten)

Day	Number of bites taken (in 5 min)			Amount of vegetation eaten (%/5 min)		
	Ants	No ants	Statistic	Ants	No ants	Statistic
1	11.2 ± 2.0	80.8 ± 3.5	$t = -17.09$ $P < 0.0001$	5.0	70.0	$U = 15.0$ $P = 0.011$
2	11.2 ± 2.6	83.6 ± 6.7	$t = -10.07$ $P = 0.0002$	30.0	75.0	$U = 15.0$ $P = 0.011$
3	11.0 ± 3.9	78.4 ± 6.9	$t = -8.52$ $P = 0.0001$	5.0	75.0	$U = 15.0$ $P = 0.011$
4	11.0 ± 4.1	100.0 ± 8.4	$t = +9.54$ $P = 0.0002$	5.0	85.0	$U = 15.0$ $P = 0.011$

On each day, the goat fed continuously for the allotted 5 min on trees uninhabited by ants. Overall, it fed for an average of 50.45 ± 8.66 s on trees that were ant inhabited (lengths of feeding bout on individual days were 54.8 ± 21.9, 78.0 ± 21.4, 36.4 ± 3.96, 30.4 ± 10.3 s).

The ants were very effective at reacting to the browsing goat. As the goat started feeding, the number and activity of ants on the outside of the plant (not just on the branch that was being attacked) increased (approximately tripling in number) and there was a distinct acrid smell of the chemical that the ants produce when alarmed. The ants moved quickly onto the goat by way of the thorns and were seen to move to and attack the more delicate areas of the face – ears, nose and around the eyes. The goat stopped feeding quickly (mean 50.45 ± 8.66 s) and would sneeze violently, shake its head and scratch its face with its hooves. After dislodging the offending ants, the goat would refuse to go back to feed on the same plant, preferring to move off to feed from another tree (this occurred in all 20 cases using ant-occupied trees). The goat did not appear to be learning to avoid ant-occupied trees unless it had already been attacked by the resident ants. It would start to feed from a new tree regardless of whether the tree was occupied by ants and would only move off once the ants had begun to attack it.

Discussion

The results show that whilst *A. drepanolobium* thorns on their own do significantly decrease the amount of damage caused by browsing mammals, further protection is afforded by the presence of symbiotic *C. nigriceps* ants.

From the observations of the goat browsing and from published data, it is clear that thorns do not stop the animal from browsing but merely slow down its rate of feeding (see also Cooper and Owen-Smith 1986; Gowda 1997). The presence of thorns makes it harder for the goat to reach the vegetation. Pairs of thorns occur every 1–2 cm along a branch (L. Stapley, unpublished data) and the goat has to take time manoeuvring its face between the thorns to take a bite. When there are no thorns, it is very easy for the animal to strip all the leaves from a branch in a relatively short period of time. The short leaves of *A. drepanolobium* also make it harder for the goat to take a bite. Similar observations have been recorded for browsing goats on *A. tortilis* (Gowda 1997).

It is interesting to note that the goat was not effectively deterred by the ants present on single branches of *A. drepanolobium*, whereas it was when it fed from a tree in situ. A larger attacking force is present on a whole tree compared to that on a single branch and ants all over the tree will react to a disturbance, not just those occupying the branch which is being attacked. Therefore, a single branch is not truly representative of the situation that occurs in the field.

The response of the goat to the defending ants was much more obvious than its reaction to the thorns, even more so when feeding from a whole tree rather than a single branch. The animal would shake its head and sneeze violently, using its hooves to remove ants that were biting its face. The ants were also very obvious in their reaction to the goat. The ants use the thorns to provide a walkway onto the animal's face and body. The ants cluster around the ends of the thorns when alarmed. As the goat tries to take a bite, it brushes against the thorns and the ants are easily brushed onto the animals' coat. When the thorns are removed it is harder for the ants to get onto the animal to administer a bite, thus making them less effective defences on their own (Fig. 1). Cooper and Owen-Smith (1986) showed that although thorns do slow down the rate of feeding, the animal will compensate for this by feeding for longer. The presence of ants overcomes this problem because the animal does not browse for long – the discomfort caused by the biting ants encourages it to quickly move on to another plant.

In areas such as Laikipia, Kenya, single colonies of *C. nigriceps* can inhabit up to six or seven *A. drepanolobium* trees (M. Stanton, personal communication); in Mkomazi, however, each *A. drepanolobium* tree is known to support one colony of ants unless branches are overlapping with neighbouring trees (L. Stapley, unpublished data). The ants only deter feeding from the particular tree on which their colony lives. The goat would not return to feed from a tree whose ants had just attacked it. It would move on and feed from another ant-inhabited *A. drepanolobium*, until it was again attacked. Prolonged exposure to ant-inhabited *A. drepanolobium* may result in a goat refusing to feed from any *A. drepanolobium*. However, observations from the field suggest that adult giraffe, for example, will continue to browse *A. drepanolobium* despite much exposure to the resident ants, although young giraffe are deterred from feeding (Madden and Young 1992).

The presence of ants on *A. drepanolobium* significantly adds to the effectiveness of thorns as a defence against browsing mammals (Table 1). This explains why the plant makes an investment in both types of defence. These observations provide support for the hypothesis that the ant-acacia relationship (on *A. drepanolobium* at least) evolved partly in response to pressure from browsing mammals (Brown, 1960).

As ants appear to be an effective defence against browsing mammals (see also Madden and Young 1992), further investigation may show that ant-acacias have invested more resources in supporting colonies of symbiotic ants rather than in other forms of defence such as chemicals (Rehr et al. 1973). Plants are known to have limited resources available to invest in defence (Coley et al. 1985) and so some difference in resource allocation may be expected between ant and non-ant-acacias. Furthermore, the role of insect herbivores cannot be ignored in the evolution of this relationship. More work is needed to highlight the importance of insects in the evolution and maintenance of this complicated interaction.

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