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Symbiotic ants as an alternative defense against giraffe herbivory in spinescent *Acacia drepanolobium*

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Summary. We explore here the occurrence of aggressive ants in an apparently symbiotic relationship with the savanna tree *Acacia drepanolobium* and their effects on giraffe herbivory on the Athi-Kapiti Plains, Kenya. Trees taller than 1.3 m were more likely to be occupied by aggressive ants in the genus *Crematogaster* than were shorter trees. Ants were concentrated on shoot tips, the plant parts preferred by giraffes. Trees with relatively more foliage had more swarming ants than did trees with less foliage. The feeding behavior of individual free-ranging giraffes on *Acacia drepanolobium* was studied. Giraffe calves exhibited a strong sensitivity to *Crematogaster* ants inhabiting *A. drepanolobium*, feeding for significantly shorter periods on trees with a greater number of aggressive ants. Older giraffes were apparently less sensitive to ants, and did not feed for shorter periods on trees with fuller foliage, despite significantly greater ant activity on these plants. The thorns of *A. drepanolobium* are significantly shorter than are the thorns of *A. seyal*, a species without symbiotic ants, a pattern that may indicate a trade-off between ants and thorns as defenses.

Key words: Acacia ants – Giraffes – Defense – Myrmecophytes – *Crematogaster* – Thorns

Myrmecophytes are plants that host ant symbionts in a mutualistic association. The protective function of ant symbionts against insect herbivores (reviewed in Beattie 1985; see also McKey 1984; Schupp 1986; Fiala et al. 1989) and vines (Janzen 1969) may provide myrmecophytes with a competitive edge, and also reduce risk of fire damage (Janzen 1967b). Although Brown (1960) and Janzen (1972) have suggested that some acacia ants may be effective against large browsers such as African antelope and elephants, the effectiveness of ants against browsing African vertebrates is unknown.

Some acacias naturally produce swellings at the bases of branches and thorns that mature into inflated-appearing 'galls' that become occupied by ant colonies. Mature galls often split with age, and ants continually colonize galls in younger portions of the tree canopy (Janzen 1966; Hocking 1970). The production of these protective chambers and nutrient-rich extrafloral nectaries are probably evolutionary adaptations to encourage ant colonization (Janzen 1972; Bentley 1977; Baker and Baker 1978; Howe and Westoby 1988).

Acacia thorns previously have been shown to be inducible defensive structures. Cooper and Owen-Smith (1986) experimentally demonstrated that spinescent structures of several woody species increase the food handling time of herbivores. Experimental and descriptive studies by Young (1987) and Milewski et al. (1991) showed that acacia thorns do serve as defenses against free-ranging giraffes, and that increased thorn length is induced by large mammal herbivory.

Plant defenses vary among plants and tend to focus on specific herbivores that cause the most damage (Rosenthall and Janzen 1979; Owen-Smith and Novellie 1982; Cooper and Owen-Smith 1986). If ant symbionts are effective against key African megafauna, then some acacia species may allocate energy in supporting and symbionts at the expense of other defenses (Janzen 1966; Madden 1988). Here we report the occurrence of symbiotic ants on *Acacia drepanolobium*, and its relationship with a major herbivore, the giraffe.

Study site and methods

Study site and species

This research was carried out in January–June 1986 and June–August 1987 at the Hopcraft Ranch on the Athi-Kapiti Plains 40 km southeast of Nairobi, Kenya. At an elevation of 1800 m, the ranch is covered by a mixture of grassland and acacia woodland

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in a semi-arid environment. Cattle and free-ranging game animals (giraffe, gazelle, wildebeest, kongoni) are harvested for sale as meat.

Acacia drepanolobium and *A. seyal* are often coinhabitants of East African grasslands (Brenan 1959; Lind and Morrison 1974). Both have bipinnately compound leaves and paired stipular thorns that become lignified soon after maturity. Leaves and stem apices are similar in relative crude protein, ash, lignin, and tannin in these species (Reed 1983). In *A. drepanolobium*, some thorns are swollen and are often inhabited by ants. Swollen thorns do not occur in *A. seyal*. *Acacia seyal* and *A. drepanolobium* are the preferred food plants of giraffes in this area (Young and Isbell 1991), and giraffes are the primary herbivores of these two acacias (Milewski et al. 1991).

Methods

Thorn length and leaf length were measured on 90 *A. drepanolobium* trees (unswollen thorns only) and 42 *A. seyal* trees of different heights up to 1.6 m. On each tree, four living branches were randomly chosen, and representative thorns and leaves measured at 0, 20 and 40 cm from the branch tip. Presence of ants on *A. drepanolobium* was scored when at least 6 ants were counted on 20 cm of a living stem tip during the sampling period. Plant height, stem circumference, weather, time of day, and location were recorded. Ant specimens were placed in alcohol. Ants were identified to genus by DM and Don Burdick of California State University, Fresno, and were deposited at the California Academy of Science.

Free-ranging giraffes (*Giraffa camelopardalis*) were observed under natural conditions, and data were collected on the time of day, sex and approximate age of the giraffe, and duration of feeding bout on a individual *A. drepanolobium* trees. This sampling was done in the morning and late afternoon, when giraffes were most active. Each feeding bout was said to begin with the initial contact of muzzle and plant, and end when the giraffe stepped away. Within one hour of each feeding bout, we placed a 0.7 m stick, whittled smooth, on a random living branch of each browsed tree and shook it with a force similar to that of feeding giraffe. We counted the number of ants that had crawled onto the stick in 5 s. The ants were brushed off and the process repeated every 15 s for four minutes, for a total of 16 counts. For each of these trees, we measured its height and estimated the percentage of branches with foliage. To increase normality, the percent foliage data were angular transformed, and the data on durations of feeding bouts and the numbers of swarming ants were log transformed.

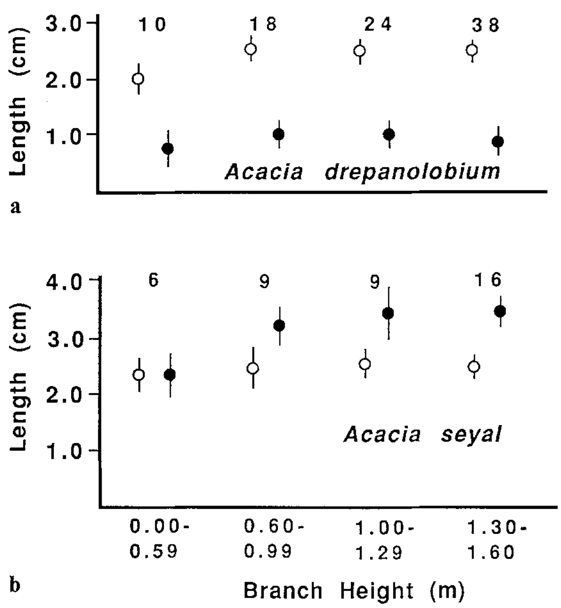

Fig. 1. (Thorn) (●) and leaf (○) lengths on **a**) *A. drepanolobium* and **b**) *A. seyal* trees of different heights. Bars represent one standard error. Numbers are sample sizes (number of trees)

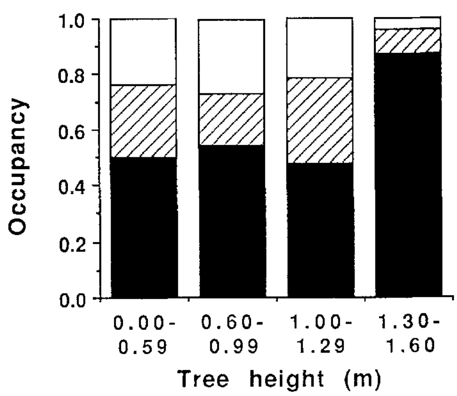

Fig. 2. Occupancy by *Crematogaster* ants (solid bars) and *Tetraponera* ants (hatched bars) on *A. drepanolobium* trees of different heights. Open bars represent trees without ants. Sample sizes ranged from 42 to 54

Results

Mean relative thorn length (thorn length minus leaf length) was significantly greater ($P<0.01$) on *A. seyal* than on *A. drepanolobium* in trees at all sampled heights (Fig. 1). Although thorns were as long as or longer than the leaves they subtended in *A. seyal*, the thorns of *A. drepanolobium* were much shorter than the leaves. In both species, leaves at all surveyed heights averaged 2.5 cm.

Ants in the genus *Crematogaster* (Acrocoelia), probably species *nigriceps* Emery, and *C. mimosae* Santschi, were significantly more likely to inhabit taller (≥ 1.3 m) than shorter *A. drepanolobium* trees ($X^2=20.7$, $p<0.001$; Fig. 2). Both species typically raise the gaster upwards and emit a distinctive odor when disturbed. They bite and then wipe their sting in the wound, producing irritation. On virtually all of the inhabited trees sampled, these ants swarmed onto the researchers' gloves and bit the gloves repeatedly, and were invasive, often reaching undergarments within minutes of plant sampling. Ants were significantly (both $p<0.001$) more abundant on young stem tips (9.6 ± 1.5 [S.E.]) than on mature stem tips (2.2 ± 0.3) or old stem tips (0.3 ± 0.2).

Tetraponera penzigi Mayr, produced small holes in galls of *A. drepanolobium*. These elongate ants sting, rather than bite, and lack the gaster erection and frantic swarming behavior of *Crematogaster* spp. *Tetraponera penzigi* ants occurred in stem tips in 10–15% of surveyed plants (Fig. 2). *Tetraponera* ants clung tightly to foliage and were reluctant to bite or to leave the host plant. When they did sting, *Tetraponera* were capable of producing irritating lesions.

Although the proportion of *A. drepanolobium* trees occupied by *Crematogaster* ants was greater in trees ≥ 1.3 m than in shorter trees, overall ant aggressiveness (measured by the stick method) was not correlated with tree height among trees browsed by giraffes ($r = -0.16$, $n = 37$, $p > 0.50$), most of which were ≥ 1.3 m. Instead, trees with more foliage had significantly more swarming ants than less foliated trees ($r = 0.43$, $n = 37$, $p < 0.05$).

The number of swarming ants per five second sampling period increased during the first 45 s of sampling, and thereafter remained constant (Fig. 3). The total numbers of swarming ants during two minute samples were not related to time of day ($r = -0.18$, $n = 37$, $p > 0.30$).

The feeding of giraffe calves was very sensitive to aggressive ants. The duration of their feeding bouts (ln sec) was strongly negatively correlated with the (ln) number of swarming ants ($r = -0.91$, $n = 7$, $p < 0.05$). In contrast, older giraffes were not obviously sensitive to ants. In fact, feeding durations of subadult and adults were positively, but not significantly, correlated with the numbers of swarming ants ($r = 0.41$, $n = 19$, $p \sim 0.10$). There was also a positive, but not significant, correlation between feeding duration of older giraffes and percent foliage ($r = 0.28$, $n = 19$, $p \sim 0.20$).

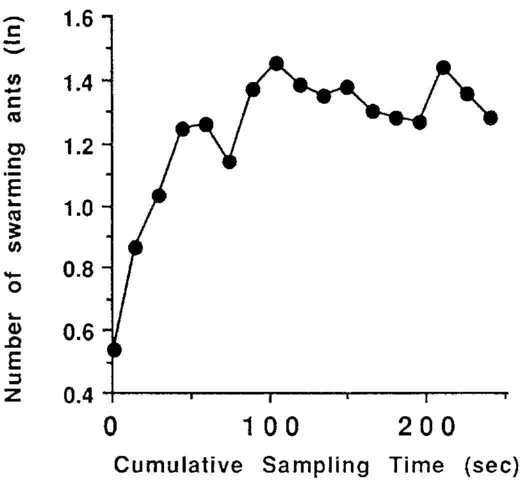

Fig. 3. The mean number of swarming ants (*log scale*) per fifteen second sampling period for the 30 browsed *A. drepanolobium* trees that had ants. Standard errors ranged from 0.140 to 0.210

Discussion

A long coevolutionary history exists between ant plants and their herbivores (Beattie 1985), and between acacias and giraffes (Dagg and Foster 1982). The nutritional quality of acacia leaves exceeds that of many less well armed coinhabitants of East African plains, and are preferred over other species by many browsers (Owen-Smith and Cooper 1987). Thorns have been shown to be a defense that can be induced by herbivory (Cooper and Owen-Smith 1986; Young 1987; Milewski et al. 1991). Ant symbionts have been posited to also have a role in defense against mammalian herbivory in thorny acacias. In Mexico, Janzen provided experimental evidence that ants in bull's horn acacia seedlings deter the rodent *Sigmodon hispidus* in the wild, and that cattle and captive brocket deer may also be deterred by ants in older acacias. However, the defensive role of acacia ants against large free-ranging vertebrates had not been demonstrated previously.

If ant symbionts are not costly features of defense for *A. drepanolobium*, then we might expect levels of spinescence similar to its close ecological and congeneric relative. *A. seyal*. However, *Acacia drepanolobium*, which hosts symbiotic ants, has significantly shorter thorns than co-occurring *A. seyal*, which does not host ants. A similar pattern of relative thorn length and ant symbioses has been observed in Central American acacias (Janzen 1966). *Acacia drepanolobium* and *A. seyal* are the two most preferred food plants of free-ranging giraffe at the study site (Young and Isbell 1991). *Acacia drepanolobium* may be able to survive with shorter thorns than *A. seyal* because it supports ant symbionts.

Aggressive arboreal ants may function as a super nettle, as suggested by Brown (1960). Swarming ants did appear to deter giraffe calves in our study. Because ant activity does increase during initial disturbance (Fig. 3), aggressive ants may be considered an inducible defense. On several occasions, we saw giraffe calves that were feeding on *A. drepanolobium* suddenly cease feeding and trot away, snorting and violently shaking their heads. Because trees with more foliage had more swarming ants, this implies that calves fed most on trees with proportionately little foliage.

In contrast, older giraffes did not feed for shorter periods on trees with more swarming ants. This does not prove that ants did not affect the feeding behavior of adult giraffes; it may be due to interactions among ant aggression, tree vigor, and giraffe preferences. For example, it is possible that adult giraffes prefer to feed on trees with more foliage despite the greater aggressiveness of the ants on these trees. Symbiotic ants on *A. drepanolobium* may well serve as deterents against older as well as younger giraffes, but experimental ant removal studies are needed in the future to separate the correlated effects of feeding bout duration, plant vigor, and ant activity.

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