Bruchid egg mortality on *Acacia farnesiana* caused by ants and abiotic factors

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Abstract. 1. This study investigated the effect of arboreal ants on the bruchid beetles that prey upon the seeds of *Acacia farnesiana* (L.) Willd., a common shrub in the savannas of Santa Rosa National Park, in northwestern Costa Rica.

2. Experiments demonstrated that ants removed an average of about 50% of unhatched bruchid eggs that had been laid on the pods of this leguminous plant. Ants also removed shells of hatched eggs.

3. In addition to the mortality caused by ant predation, about 30% of the eggs disappeared before hatching, presumably due to the combined effects of temperature and wind.

4. The orientation of the branch on which a pod was located did not affect the proportion of eggs lost from that pod.

Key words. *Acacia farnesiana*, Bruchidae, bruchid egg mortality, predator ants.

Introduction

Ants have long been known to influence the composition of the insect fauna on plants (e.g. Hinds, 1907; Carroll & Janzen, 1973; Schemske, 1980; Heads & Lawton, 1985; Grant & Moran, 1986). They have been reported to interfere or interrupt oviposition by other insects such as flies (Inouye & Taylor, 1979; Schemske, 1980), to harvest larvae, usually of Lepidoptera (e.g. Bentley, 1977; Stephenson, 1982; Campbell & Torgensen, 1983), and to attack adults of chrysomelid beetles (Messina, 1981). However, predation by ants on insect eggs has not been well studied, and although it has been reported in some cases (e.g. Hinckley, 1961; Bentley, 1977; Stephenson, 1982), available data are few (Nickerson *et al.*, 1977; Risch, 1981; Robertson, 1988), even for intensively studied forest insects (Torgensen & Mason, 1987).

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While studying seed predation by bruchid beetles on *Acacia farnesiana* (L.) Willd. (a non-obligate ant-acacia) in Santa Rosa National Park, Costa Rica, I observed ants on branches carrying unhatched bruchid eggs and sometimes empty egg shells. In order to measure bruchid egg mortality due to ant predation, I designed an experiment to compare egg losses from branches from which ants had been excluded with losses from branches where ants could forage freely. The fates of both unhatched and hatched eggs were determined. Egg disappearance from branches where the presence of ants was prevented was presumably due to abiotic factors such as high temperatures and wind (or the combined effect of both) because no other animals were seen removing the eggs.

Materials and Methods

Study area. The study was conducted in Santa Rosa National Park, northwestern Costa Rica. The vegetation is tropical dry forest, with patches

of evergreen oak forest and pastures in the uplands (300–350 m of elevation). The pastures or savannas are dominated by *Hyparrhenia rufa* (Mees.), an introduced African grass. It is in these savannas where *Acacia farnesiana* is found, being very abundant in some places. Fieldwork took place in the dry season of 1988, from 30 March to 14 May, although preliminary observations were made during the same season in 1987. The average temperature from March to May in 1987 and 1988 was *c*. 34°C. Winds (blowing mainly from the northeast) are important in the dry season, especially during the first half. The wind speed averages between 10 and 30 km/h, at times reaching 90 km/h.

Study organisms. The indehiscent fruits of *A.farnesiana* are 5–6 cm long and contain an average of eleven seeds which measure 5–7 mm in diameter. The fruit crop size varies greatly among shrubs, ranging from *c*. 50 to 2000 pods (Traveset, 1989). The fruiting period is usually from January to May, although it can start in late October and last until early July. Asynchrony in fruiting is widespread among and within shrubs.

The larvae of two species of bruchid beetles (Bruchidae), *Mimosestes nubigens* (Mots.) and *Mimosestes mimosae* (Fab.), the latter less common, eat the seeds of *A.farnesiana* before they are dispersed. Both bruchids lay their eggs on green as well as ripe pods on the shrub, and also on fallen pods beneath the plant. The eggs appear identical in both species; they are *c*. 1 mm in diameter and appear transparent-yellowish. They are usually laid in the sutures, crevices or wounds commonly made by sucking Hemiptera in fruits. Within 5–10 days after oviposition, the eggs hatch and the first instar larvae drill through the pod valve, entering the seeds where they feed for about a month. The adults emerge (one per seed) after several days of pupation.

In the study area, *A.farnesiana* harboured at least four species of ants in 1987–88: *Cremato-gaster brevispinosa* Mayr was the most common, followed by *Camponotus* cf. *planatus* Roger, *Camponotus rectangularis* Emery and *Pseudo-myrmex sericeous* Mayr. Not all species of ants were seen on an individual shrub, and in some of the shrubs, ants were rare or absent. Species of these three genera are usually found foraging in flower bases with well-developed nectaries (Janzen, 1983). *C.brevispinosa* is a common,

aggressive, tree-nesting ant in Costa Rica (Carroll & Janzen, 1973). Although all four species of ants found on the shrubs may prey on bruchid eggs, I observed removal only by *C.brevispinosa*. Ants of the genus *Camponotus* have also been found removing eggs laid on Douglas-fir trees by the lepidopteran *Orgyia pseudotsugata* (Torgensen & Mason, 1987).

Experimental design and procedure. In the laboratory, about fifty females of *Mimosestes nubigens* were allowed to oviposit on intact, mature pods of *A.farnesiana*, chosen arbitrarily from several different shrubs. Females were left with the pods in small plastic jars for a maximum period of 3 days. My observations (Traveset, 1989) showed that the maximum number of bruchid eggs laid on a pod on a shrub was thirty-three; however, the number observed is usually very much lower, possibly due to previous egg removal.

Two hundred pods with eggs were hung on ten *A.farnesiana* shrubs where at least one ant had been seen. For each shrub, twenty pods were haphazardly distributed in four groups of five pods. Each group was hung on a different branch. The chosen branches were oriented in a different compass direction (N, E, S or W) and were approximately at the same height (*c*. 2 m). Pods were tagged and fastened to the branches by thread. A 10 cm wide band of tape was wrapped around the base of two of the branches, and a sticky resin (tree tangle-foot) was sprayed on the tape to prevent ants from gaining access to the pods. The other two branches were used as controls. The treated branches were chosen so that they did not touch other branches or adjacent vegetation that might form bridges for the ants. Treated branches were inspected every 3–4 days to ensure that the tangle-foot barrier was still intact.

After 5 days the number of remaining bruchid eggs was recorded. Eggs recently laid by bruchids were readily distinguishable by their transparency and softness; they represented less than 5% of the eggs present on the pods (in experimental as well as in control branches) and were included in the counts. Pods were checked again 10 days later, and were removed from all but three shrubs. In these three shrubs, pods were left for 15 more days to determine what proportion of egg shells remain a month after oviposition.

Statistical analysis. Three two-way ANOVAs

were performed to compare differences among shrubs and between control and experimental branches in each of the following variables: (1) number of eggs present per pod at the start of the experiment (to check that treated and control branches did not differ on day 0), (2) proportion of eggs removed per pod during the first 5 days, and (3) proportion of eggs removed per pod during 15 days. The effect of branch orientation on egg mortality due to abiotic factors was determined in a one-way ANOVA where only treated branches were considered. Arcsine transformations were used to normalize the proportions.

An estimate of egg mortality per shrub due only to ant predation was obtained by subtracting the percentage of eggs removed during the first 5 days after pods were hung in tanglefoot treated branches from that in control ones (where removal was due to the combined effect of ants and environmental factors). The possibility that non-flying insects other than ants preyed on bruchid eggs seems unlikely since ants were the only egg predators found stuck in the resin. Flying insects might remove eggs from the fruits; however, this was not observed and no reports were found in the literature.

Results

At the beginning of the experiment, the number of eggs per pod on control and experimental branches did not differ (Fig. 1). After 5 and 15 days of pod placement on the branches, the proportion of eggs missing from control branches was significantly greater than the proportion missing from pods on branches treated with tangle-foot ($F_{1,9}=18.21$, $P<0.01$, at day 5, and $F_{1,9}=33.83$, $P<0.001$, at day 15; Fig. 1).

The shrubs differed significantly in the intensity of egg removal per pod ($F_{9,180}=10.81$ and $F_{9,180}=6.36$, $P<0.001$, at days 5 and 15, respectively). There was also a significant interaction between shrubs and treatments ($F_{9,180}=15.29$ and $F_{9,180}=6.17$, $P<0.001$ at days 5 and 15, respectively), i.e. not all shrubs had the same proportion of eggs lost from control and experimental branches (Table 1). In two shrubs (numbers 2 and 10), the difference between control and experimental branches was not significant ($P>0.05$).

Ants were responsible for removing an average of 45.2% of the eggs from each shrub. Egg mortality caused by ants ranged from 7% to 92% among shrubs. Assuming that the day of pod placement was roughly equivalent to the day of oviposition by the female bruchids in nature, and considering the *c.* 30% of egg loss to environmental agents, this means that only about 25% of eggs laid by the beetles survive until the fifth day.

Even after the larvae had entered the fruits, egg shells (which probably retain some nutritive value for predator insects) continued to be removed. Fifteen days after fastening the pods to the branches, no egg shells remained on the control branches in half of the shrubs, while in the other half the number remaining ranged from three to seventeen eggs per pod, representing an average intensity of removal of $87.3\pm4.7\%$ ($n=10$ shrubs). In contrast, in the treated branches the number of remaining shells was still about half ($53.4\pm4.3\%$, $n=10$) the number of laid eggs (Fig. 1). A month after pod placement, the percentage of egg shells remaining per pod ranged from 13% to 34% in control branches and from 47% to 59% in the experimental ones.
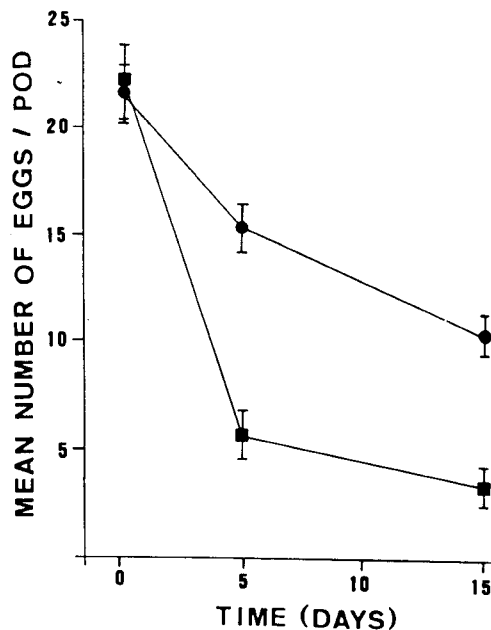

Fig. 1. Mean number of bruchid eggs per pod in control (■) and experimental (●) branches at days 0, 5 and 15 on a pod basis. Error bars represent ±1 SE. $n=100$ pods.

Table 1. Mean and standard error of the number of eggs per pod originally present (day 0), and of the percentage of eggs missing per pod after 5 and 15 days. Each mean is based on ten pods. C: control; E: experimental.

Shrub	Branch	Eggs at day 0	% Eggs missing at day 5	% Eggs missing at day 15
1	C	12.0 ± 3.3	23.1 ± 5.5	73.9 ± 9.0
	E	13.7 ± 3.1	16.2 ± 4.9	34.7 ± 8.8
2	C	35.0 ± 6.7	46.5 ± 10.9	62.6 ± 9.5
	E	24.9 ± 4.4	31.5 ± 9.8	43.7 ± 9.5
3	C	42.9 ± 9.6	80.2 ± 7.7	85.0 ± 6.5
	E	32.9 ± 7.1	41.4 ± 6.8	52.7 ± 7.4
4	C	12.0 ± 1.5	100.0 ± 0.0	100.0 ± 0.0
	E	17.4 ± 3.3	13.7 ± 4.7	39.9 ± 7.1
5	C	26.6 ± 3.4	81.4 ± 7.8	84.5 ± 7.2
	E	21.6 ± 2.2	29.7 ± 7.9	60.1 ± 8.0
6	C	22.1 ± 5.6	99.1 ± 0.9	100.0 ± 0.0
	E	31.6 ± 2.0	6.6 ± 1.7	59.7 ± 4.3
7	C	21.2 ± 2.0	89.7 ± 4.0	99.5 ± 0.5
	E	13.8 ± 2.2	54.1 ± 6.1	76.6 ± 5.5
8	C	14.3 ± 3.2	100.0 ± 0.0	100.0 ± 0.0
	E	16.4 ± 3.1	24.3 ± 5.6	39.6 ± 6.6
9	C	22.6 ± 1.6	91.4 ± 3.1	100.0 ± 0.0
	E	21.6 ± 2.2	48.0 ± 6.0	61.1 ± 5.1
10	C	13.9 ± 1.8	54.3 ± 7.5	67.3 ± 7.7
	E	23.3 ± 5.6	48.3 ± 10.6	65.5 ± 7.9

No differences in mortality were found between branches facing different compass directions neither at day 5 or 15 ($P>0.05$).

Discussion

Ants appeared to be responsible for killing on average 45% of the eggs laid by bruchids on the pods of *A.farnesiana*. This occurred within the first 5 days after pods were placed on the branches. Additional eggs may have been removed later, before hatching. This estimate is higher than that reported by Hinckley (1961) from Hawaii, where *A.farnesiana* is introduced. Hinckley estimated that about 40% of the bruchid eggs were presumably lost to ants of the genus *Monomorium*. The large egg predation by ants on the shrub contrasts with very low predation beneath it (Traveset, 1989) and thus may represent a selective factor favouring bruchid females that oviposit on fallen fruits. However, there are other biotic and abiotic factors which act in the opposite direction (Traveset, 1989).

About 30% of the bruchid eggs were lost from the branches where ants had been excluded. The high temperatures (which can sometimes reach around 45°C in the shade) combined with the wind presumably cause eggs to desiccate and subsequently fall. Many of the eggs laid on pods of *A.farnesiana* in nature are found in the unexposed valve, inside crevices, next to ridges or within wounds. Oviposition on these sites may well decrease egg losses to abiotic factors. Branch orientation did not affect the loss of eggs to abiotic factors probably because all branches are similarly moved by wind and exposed to sun, since the canopy of *A.farnesiana* is rather diffuse.

Egg removal varies from shrub to shrub, perhaps depending on the density of ants foraging on the shrub and the resistance of the branches to the wind. Even within an individual plant, ants might not forage equally on the lower and upper parts, as has been found for other plants

by Nickerson *et al.* (1977) and by Campbell & Torgensen (1983).

From the point of view of *Acacia farnesiana*, ants defend the seeds from predators. Whether the plant–ant interaction is mutualistic or commensal remains unknown. In other plants, such as ant-acacias, ants might well reduce seed predation by insects in addition to defending the plant from herbivores. The evolution of strong mutualistic relationships between ants and plants may, in some cases, have started with an interaction such as that described in this study, with ants defending the plant's seeds rather than the plant itself.

Acknowledgments

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