Pre-dispersal seed predation in Central American *Acacia farnesiana*: factors affecting the abundance of co-occurring bruchid beetles

Anna Traveset*

Department of Biology, University of Pennsylvania, Philadelphia, PA 19104–6018, USA

Summary. Pre-dispersal seed predation of the leguminous *Acacia farnesiana* by *Mimosestes nubigens* and *M. mimosae* (Coleoptera: Bruchidae) was investigated in Santa Rosa National Park, northwestern Costa Rica. The purpose of the study was to determine the patterns of resource utilization by the seed predators and the mechanisms causing such patterns. Immature, mature, and fallen fruits were monitored during the dry seasons of 1987 and 1988 from different shrubs and areas. Parameters describing plant size, fecundity, and relative plant isolation were measured on each shrub. No evidence of spatial or temporal segregation was found between the two species and the intensity of seed predation was independent of the variables measured from each plant. *M. mimosae* was scarcer and always occurred with *M. nubigens*. Both were present in areas with low and high densities of the host plant, and the frequency distributions of their emergences from the fruits overlapped through the fruiting season. *Urosigalphus* sp., a hymenopteran parasitoid, represented ca. 40% of all insect emergences in 1987 and ca. 30% in 1988. This wasp attacked a greater proportion of bruchid eggs on pods on the shrub than on pods beneath it, and more on green than on mature fruits. Parasitism thus appears to select against bruchid females that oviposit at an early stage of pod maturation. The harsh conditions of the dry season, namely heat and desiccation, also accounted for a high level of bruchid pre-emergence mortality, especially in fallen fruits, where survival from egg to adult was only about 18%. Beneath the shrubs, bruchid females exhibited selectivity, ovipositing more on pods in the shade than on those exposed to direct sunlight. In contrast to parasitoids, abiotic factors probably impose a selective force against those bruchid females that oviposit at a late stage of maturation or on pods already dropped. Both bruchid species can have more than one generation during the fruiting period. The intensity of seed predation did not, however, change during the season. The data obtained in this study suggest that factors like natural enemies and severe weather are more likely to limit the bruchid population densities than intra- or interspecific competition.

* *Present address:* Estación Biológica de Doñana, Apartado 1056, E–41080 Sevilla, Spain

Offprint requests to: Institut d'Estudis Arançats de les Illes Balears, Crtra. de Valldemosa. Km. 7'5, Palma de Mallorca, Spain

Seed predation by insects provides a good system for the study of interactions among species using a common resource that is potentially limited. Yet, despite the long list of plants that harbor more than one species of insect seed predator (e.g., Janzen 1980), little is known about how the insects co-occur (but see Janzen 1971a, 1977; Johnson 1981; Pellmyr 1989) and what factors determine the relative intensities of seed predation by the different species. Although interspecific competition among insect seed predators has been claimed in at least one study of a natural community (Johnson and Slobodchikoff 1979), no evidence exists of competitively structured insect guilds. In general, interspecific competition appears to be infrequent in insect communities (e.g., Strong et al. 1984 and references therein; Fritz et al. 1987; Lawton and Gaston 1989; Juliano and Lawton 1990; Loreau 1990), and other factors such as parasitism, predation, plant phenology, weather, and migration probably play a more important role in insect population dynamics.

This study investigated the interactions between two species of pre-dispersal seed predators on *Acacia farnesiana* (L.) Willd. (Fabaceae: Mimosoideae) and aimed to determine the importance of different biotic and abiotic factors that affect their population dynamics. The questions addressed were the following: (1) Are the bruchid species spatially and/or temporally segregated through differences in their oviposition patterns? (2) How intense is parasitoid attack and how does it affect seed predation? (3) Do abiotic factors such as heat and desiccation influence bruchid survival in the seeds? (4) Since both insect species are multivoltine, does the intensity of seed predation vary through the fruiting season?

Study site and natural history

The study was conducted in Santa Rosa National Park, Guanacaste Province, northwestern Costa Rica, during the dry seasons of 1987 and 1988 (some preliminary data

were gathered in 1986). Santa Rosa consists of about 10,800 ha (0–350 m elevation) of mainly deciduous forest with small patches of evergreen forest of *Quercus oleoides* Cham. & Schlecht. and with large patches of artificial savannas (or pastures) in the upland plateau. These savannas are dominated by the introduced African grass *Hyparrhenia rufa* (Mees.), and trees of *Crescentia alata* HBK. and *Acacia farnesiana* are usually found in them. A detailed description of the habitats and vegetation of the Park can be found in Hartshorn (1983).

Santa Rosa receives an average annual rainfall of 1500–2000 mm, virtually all of which falls between mid-May and December. Winds are an important component of the climate, especially during the first half of the dry season. The average maximum temperature from January to May during the 2 years of the study was about 34 °C, and the highest temperatures were recorded in April (up to 40 °C in the shade).

Acacia farnesiana densities range from isolated individuals (1 indiv./ha) to around 60–70 indiv./ha. They usually occur in small patches scattered through the savanna, but are sometimes at the very edge of the forest. This study was carried out in four different areas on the plateau of Santa Rosa. These areas are described in detail in Traveset (1989).

Acacia farnesiana is native to Central America, although it currently ranges from southern United States to Argentina and has also been introduced into the Old World Tropics (Little and Wadsworth 1964). The growth form ranges from small shrubs of 0.5 m to highly branched and spreading trees up to 5–6 m tall. The plant begins producing tiny yellow flowers usually in November-December but can start as early as September and continue until February-March. Small green fruits are visible about 5–6 weeks after pollination and require approximately 1 month to reach full size. Full-sized fruits take an average of 18.7 ± 2.4 (SD) days to mature (i.e. to turn brown and hard), and an average of 16.0 ± 3.5 (SD) days to be dropped ($n = 800$ pods from 32 plants). Asynchrony in fruiting is widespread both within and among individuals. Fruit crop per plant during 1987 and 1988 ranged from less than 50 to around 2000 pods. Janzen (1975a) gives much higher estimates for plants in Palo Verde, Costa Rica.

The dark brown pods are indehiscent, 4–12 cm long and 0.5–1.5 cm broad, thick-walled and only slightly constricted between the seeds. Up to five pods can be found on a stalk; if there are more, they usually abort. Pods contain sweetish and scented pulp. Inside each fruit there is an average of 11 seeds ($n = 52$ shrubs), ranging from 2 to 15. These seeds are elliptic and slightly flattened, 5–7 mm long, and are covered by a very thick endocarp.

The main dispersers of *A. farnesiana* seeds in Santa Rosa currently are horses, white-tailed deer and ctenosaurs (Traveset 1990a). The proportion of undispersed fruits varies greatly among shrubs; often, large quantities of pods accumulate beneath the plant during the season. The undispersed pods rot soon after it rains in May.

Three species of bruchid beetles feed upon the seeds of *A. farnesiana*: *Mimosestes nubigens* (Mots.), *M. mimosae* (Fab.) and *Stator vachelliae* Bott. None is restricted to a single host species (Janzen 1980; Johnson 1980, 1983, 1984), but the other known hosts do not occur in Santa Rosa or within the habitat where *A. farnesiana* is found (pers. obs.). The two *Mimosestes* species are pre-dispersal seed predators, whereas *S. vachelliae* attacks the seeds after dispersal (Traveset 1990b).

The two species of *Mimosestes* can have more than one generation per fruiting season (Janzen 1975a, and pers. obs.). Females oviposit only on full-sized fruits, usually on the sutures of the pods, in crevices on the valves, and on or near wounds made by sucking hemipterans. Eggs of both species are about 1 mm long, transparent and glued to the valve, isolated or rarely in clumps, and appear identical under a dissecting microscope. Within 5–10 days of oviposition, the eggs hatch and the larvae drill through the pods and then into the seeds where they pass through at least three instars (Hinckley 1960) during the next 4–5 weeks. After several days of pupation, the adult emerges, cutting a round hole through the seed coat and another one through the pod wall. Even if more than one larva enters a seed, only a single adult emerges. Soon after emergence, bruchids mate and females begin ovipositing; a single female can lay up to 120 eggs (unpubl. data).

At least five species of parasitoid wasps attack the bruchids: *Urosigalphus* sp., *Bracon* sp. (Braconidae), *Lariophagus* sp. (Pteromalidae), *Eupelmus* sp. (Eupelmidae) and *Horismenus* sp. (Eulophidae). Their degree of host specificity is unknown. Females of *Urosigalphus* sp., by far the most common species, search on the pods for fresh bruchid eggs and oviposit inside them. The wasps' developmental time is the same as that of the bruchids. The much scarcer *Bracon* sp. attacks the bruchid larvae within the green, tender pods. *Eupelmus* sp. was occasionally found emerging from mature *A. farnesiana* seeds. These three species are solitary wasps, whereas *Lariophagus* sp. and *Horismenus* sp. are smaller and gregarious, and up to eight individuals can emerge from a single seed (pers. obs.).

Material and methods

Frequency distributions of the insects

During the dry season of 1987, I arbitrarily chose a total of 32 *A. farnesiana* individuals from the four study sites (14 from area 1, 9 from area 2, 2 from area 3, and 7 from area 4). In order to evaluate the bruchid and wasp incidence and distribution on green, mature and fallen fruits, I monitored three stages of pods from each plant as follows: 25 green pods were labelled when they had reached full size and were collected on the day of maturation; at this time, another 25 green pods that were beginning to mature were marked, and they were collected subsequently on the day they were shed; finally, after most ripe marked fruits were shed, 25 pods that were ready to fall were collected and labelled, and then mixed with other fallen pods beneath the plant and left for a further 15 days. Preliminary observations indicated that 15 days was the average time needed for pods to become completely dry, and for the female bruchids to stop ovipositing on them.

For each fruit collected I recorded the following variables: length, number of days exposed to bruchids, number of eggs on its surface, and number of insect exit holes already present. Pods were placed in individual bags and checked daily for emerging bruchids

or parasitoids. For every emergence I recorded the number of days since the pod had been collected. Once all insects had emerged, I dissected each pod and recorded the total number of seeds in it and the number of seeds damaged by larvae.

The number of insects emerging from mature fruits but coming from eggs laid at the green stage had to be subtracted in order to determine the intensity of seed predation on ripe fruits. I estimated the time of egg laying with the following inequalities:

if $T_{AM} + T_E < D_T$, the egg was laid at the green stage, and
if $T_{AM} + T_E > D_T$, the egg was laid at the ripe stage, where $D_T =$ the average developmental time of bruchids, $T_E =$ the time that each bruchid took to emerge since pod was collected, and $T_{AM} =$ the time that the individual pod was available to bruchids at the mature stage.

I did the same with the bruchid emergences from fallen pods. In this case, time that pods were available to bruchids was constant since all fruits were left beneath the shrub for 15 days. The appropriate inequalities, therefore, were:

if $15 + T_E < D_T$, the egg was laid on a green or ripe pod
if $15 + T_E > D_T$, the egg was laid on a fallen pod

I estimated bruchid developmental time by rearing in the laboratory a total of 30 females (20 *M. nubigens* and 10 *M. mimosae*). Each female was allowed to oviposit on different mature pods. I reared bruchids twice during the fruiting season (in February and in May), using different females each time, to check for a possible change in the developmental time with environmental conditions.

Height of the plant, canopy diameter, total fruit crop size and average distance to the nearest three fruiting *A. farnesiana* neighbors were recorded for all experimental plants. I also recorded the total number of pods beneath the shrub on the day on which pods were placed on the ground and on the day on which pods were collected, to determine whether the quantity of pods had an effect on bruchid oviposition on them. In order to know whether the exposure of fallen fruits to sun had an effect on oviposition and pre-emergence bruchid mortality, I gave one of three indices to each labeled pod: 1 = complete exposure, 2 = partial exposure, and 3 = no exposure (constantly under shade).

In the dry season of 1988, I monitored the fruits of 20 individuals of *A. farnesiana*. I chose two asynchronous groups of 10 shrubs from the areas used in 1987. The first group had full-sized green pods in February (they were the first to produce fruits this season in the study areas) while the second did not have green pods until mid-March or beginning of April. Although all 32 shrubs used in 1987 fruited again in 1988, I monitored only 9 of them the second year. The methods employed were basically the same as in 1987 except that I measured the incident light beneath the plant, to determine the exposure to sun of fallen pods, using a portable light-meter on two clear and consecutive days in April, between 11:00 and 12:00 a.m.

Bruchid survival at the three fruit stages

Since the eggs of *M. nubigens* and of *M. mimosae* appeared indistinguishable, bruchid survival was calculated for both species pooled. Egg survival per pod was the number of eggs that hatched on a pod relative to the total number of eggs present on it. Survival from larva to the adult stage was estimated as the number of adult emergences relative to the number of pod entrance holes made by the first-instar larvae. I determined bruchid survival at each of the three fruit stages from 8, 9, and 12 shrubs respectively, studied in 1987. For the mature fruit sample, survival was underestimated since the number of eggs considered were both those laid at the green and at the mature stage. For the fallen fruit sample, the exact number of eggs laid at this stage could be determined because the number of eggs present on the day of pod placement on the ground had been previously recorded. In 1988, I calculated survival only from the pods beneath the 20 shrubs monitored, again considering just the eggs laid at this stage.

Intensity of seed predation per shrub

I estimated this parameter as the proportion of damaged seeds present in the 25 pods collected beneath each shrub once all bruchids and wasps had emerged. Damaged seeds did not include those aborted or sucked by hemipterans, but only those that had a bruchid or wasp exit hole and those where the insect had died at a late stage of development (identifiable by a dark spot on the seed coat). Since larvae that died at an early stage were not detected, the intensity of seed predation per shrub was probably underestimated. If the larva has not eaten the embryo or most of the cotyledons, however, the seed may still germinate (cf. Lamprey et al. 1974).

Data analysis

All ANOVAs were carried out using the GLM procedure in SAS (SAS 1985). The relationships among the variables measured for each individual plant were analyzed by Pearson's correlation (unless otherwise indicated).

Results

Spatial and temporal distribution of the two bruchid species

The mean bruchid developmental time was 33.6 ± 2.41 days, and did not differ between the two species, seasonally or among females. Significant differences in D_T were found only among pods ($P < 0.01$), suggesting that some trait(s) of the individual fruits or seeds determine how long the bruchids take to emerge. From the fruits monitored in the field, *M. nubigens* emerged much more frequently than *M. mimosae* in both years of the study (Fig. 1). In 1987, abundances did not differ among the four areas for either species, but did differ significantly among shrubs within each area (Table 1A); some shrubs were attacked only by *M. nubigens*, although most also bore *M. mimosae*. *M. nubigens* emerged with the same frequency from the three fruit stages, whereas *M. mimosae* emerged more frequently from green pods than from pods collected at the other stages (Table 1a). For both species, there was a significant interaction between shrub and pod stage within an area; i.e., shrubs within an area differed in the pod stage at which bruchid attack was the greatest.

The 1988 results were similar to those of 1987, except that no significant differences were found among stages in the number of emergences of *M. mimosae* per pod (Table 1b). The frequency of bruchid emergences per pod did not vary during the fruiting season either (Table 1B). *M. mimosae* was possibly more abundant in the first than in the second half of the season, although the difference was not significant ($P = 0.08$), perhaps due to the very low number of emergences.

The number of emergences was not correlated with plant height, canopy diameter, fruit crop size, average fruit length, average number of seeds per pod, or average period that green and mature pods were available to bruchids, for either species and either year (all P values > 0.05). In 1988, relative plant isolation seemed to be correlated with the number of *M. nubigens* emergences ($r = 0.48$, $P < 0.05$, $n = 20$), but the significance was lost when the other plant variables were controlled in a par-

Table 1. ANOVA of the number of emergences per pod of *Mimosestes nubigens,* *M. mimosae,* and *Urosigalphus sp.* in 1987 (above) and 1988 (below). Area and shrub are random effects whereas time and stage are fixed effects. **a (b)** means that **a** is nested within **b**. Data are square-root transformed

a

Source	df	M. nubigens		M. mimosae		Wasps	
		MS	F	MS	F	MS	F
1987							
Area	3	2.33	0.82	0.02	0.07	0.48	0.79
Shrub (Area)	28	2.85	11.88***	0.29	4.83***	0.61	4.07***
Stage	2	1.99	2.88	0.79	9.88*	16.43	34.23***
Area × Stage	6	0.69	0.93	0.08	0.53	0.48	1.23
Stage × Shrub (Area)	56	0.74	3.08***	0.15	2.50***	0.39	2.60***
Error	2303	0.24		0.06		0.15	
b							
1988							
Time	1	0.10	0.06	0.13	3.25	0.002	0.003
Shrub (Time)	18	1.68	6.00***	0.04	2.50***	0.72	6.37***
Stage	2	0.09	0.11	0.02	0.67	3.43	14.29***
Time × Stage	2	0.55	0.70	0.02	0.67	0.34	1.42
Stage × Shrub (Time)	36	0.79	2.82***	0.03	1.88**	0.24	2.12***
Error	1405	0.28		0.016		0.113	

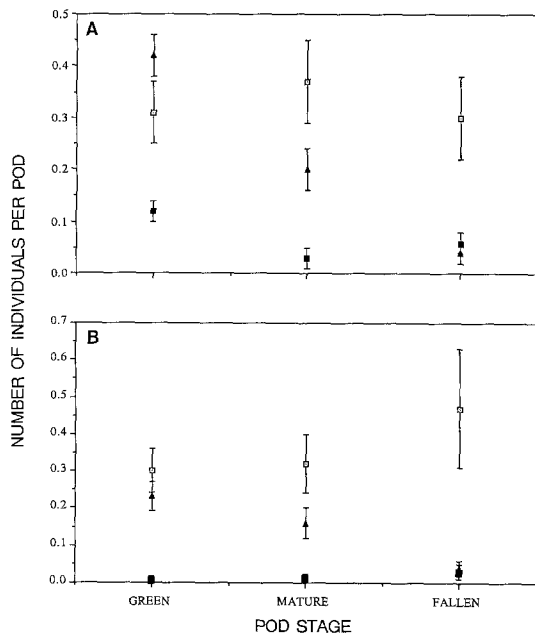*** $P < 0.001$; ** $P = 0.001$; * $P = 0.01$

Fig. 1A, B. Number of *Mimosestes nubigens* (□), *M. mimosae* (■), and parasitoid wasps *(Urosigalphus sp.)* (▲) that emerged per pod from eggs laid at each of the three fruit stages during the dry seasons of **A** 1987 and **B** 1988. Two-standard-error *bars* are shown above and below the mean

Table 2. Mean and standard error of the proportions of (1) bruchid eggs that survived to larvae, (2) larvae that survived to adults and (3) eggs that survived to adults, at the three pod stages. Data from 1987 dry season. At each stage 25 pods from each shrub are considered. For each variable, means with the same superscript letter are not significantly different (GT2 test)

Stage	n (shrubs)	(1) ± SE	(2) ± SE	(3) ± SE
Green	8	0.55 ± 0.09[a]	0.85 ± 0.10[a]	0.45 ± 0.08[a]
Mature	9	0.56 ± 0.06[a]	0.60 ± 0.09[b]	0.36 ± 0.07[a]
Fallen	12	0.36 ± 0.08[a]	0.54 ± 0.08[b]	0.20 ± 0.04[b]

tial correlation analysis. Neither the number of eggs laid on fallen pods or the number of bruchids that emerged from them were associated with the quantity of pods beneath a plant.

Parasitoids

In the 2 years of the study, the intensity of parasitism by *Urosigalphus* sp. was significantly different among pod stages (Table 1a, b). This wasp attacked significantly more bruchid eggs laid on the shrub than beneath it, and more on green than on mature fruits (Fig. 1). No differences were found among areas (Table 1a) or between the first and second half of the fruiting season (Table 1b). The abundance of *Urosigalphus* sp. varied significantly among shrubs in both years. In 1987, this wasp represented on average $38.7 \pm 2.49\%$ ($n = 32$ shrubs) of all insect emergences per shrub, ranging from 10 to 69%. In 1988, the range was 5–56% with an average of $30.4 \pm 3.1\%$ ($n = 20$ shrubs). In some shrubs, the number of wasps emerging even surpassed that of bruchids. Furthermore, not all shrubs within an area (Table 1a) and at a given time of the season (Table 1b) had the same intensity of parasitism at a particular pod stage.

The number of wasp emergences per shrub was not correlated with any of the plant parameters measured ($P > 0.05$), but was positively correlated with the number of *M. nubigens* emergences, in 1987 ($r = 0.67$, $P < 0.001$, $n = 32$) and in 1988 ($r = 0.55$, $P = 0.01$, $n = 20$). This correlation was also significant in a partial correlation analysis. However, no evidence of density-dependent parasitism was found, i.e., the proportion of insect emergences that were wasps was not associated with the number of bruchid emergences.

The remaining wasp species were rarely found, representing less than 1% of all insect emergences in both years.

Table 3. Mean and standard error of the number of bruchid eggs laid and the number of emergences, on a pod basis, for each index of exposure to sun. Data from 1987 dry season. For each variable, means with the same superscript letter are not significantly different (GT2 test)

Exposure to sun	n (pods)	$\bar{x}$ Ovip. pod $\pm$ SE	$\bar{x}$ Emerg. pod $\pm$ SE
Total	437	0.93 ± 0.14^a	0.33 ± 0.06^a
Partial	337	1.55 ± 0.22^b	0.38 ± 0.07^a
None	26	4.23 ± 1.70^c	0.85 ± 0.50^b

Effect of abiotic factors on bruchid survival

Egg survival did not vary significantly among pod stages $(F_{2,28} = 2.04, P = 0.15)$, whereas survival from larva to adult was significantly higher in green than in mature or fallen pods $(F_{2,27} = 5.03, P = 0.01)$, and survival from egg to the adult stage was significantly lower in fallen fruits than in fruits on the shrub $(F_{2,28} = 4.57, P = 0.02)$ (Table 2). Exposure of fallen fruits to sun significantly affected the number of bruchid eggs laid on them and the number of bruchid adults emerging from them $(F_{2,31} = 7.27$ and $F_{2,31} = 5.25$, respectively, $P < 0.01$; Table 3). In 1988, the incident light measured under the shrubs was also negatively correlated with both bruchid oviposition $(r_s = -0.53, P = 0.02, n = 20$ shrubs) and emergences $(r_s = -0.52, P = 0.02, n = 20$ shrubs). Egg survival was independent of incident light level $(r_s = -0.002, P > 0.05, n = 15)$, but survival from larva to adult decreased with increasing light $(r_s = -0.77, P < 0.001, n = 11$ shrubs). Only an average proportion of 0.16 ± 0.04 of the eggs laid on fallen pods in 1988 survived to adults.

The number of eggs laid on a fallen pod was sometimes higher than the seeds available inside (up to 86 eggs were found on a pod). In all such cases, the pods were protected from direct sunlight. However, only $16.2 \pm 5.4\%$ ($n = 15$ pods with eggs) of the eggs laid on the unexposed pods survived to adult. It is unknown whether all eggs on a pod had been laid by a single female; this seems unlikely, however, since all the eggs were not laid on the same day, but throughout the 15 days pods were on the ground (unpubl. data).

Shrubs differed in the number of eggs laid by bruchids on fallen pods $(F_{2,33} = 10.64, P = 0.001)$, and in the number of adult insects that emerged from them $(F_{2,33} = 10.56, P = 0.001)$. There was also a significant interaction between shrub and exposure in bruchid oviposition $(F_{33,733} = 2.80, P = 0.001)$, but not in emergences $(F_{33,733} = 1.19, P > 0.05)$. The shrubs that produced a denser canopy, or were near trees of other species that cast shade on the fallen pods, usually suffered most predation at this stage.

Intensity of seed predation per shrub

Shrubs varied greatly in the intensity of seed predation in both fruiting seasons, with no apparent seasonal pattern. The values ranged from 0.33 to 36.59% in 1987, and from 0.01 to 37.82% in 1988. There was no consistency between years in the nine shrubs used both in 1987 and 1988, and intensity of seed predation was not correlated with any of the variables measured from each plant.

Discussion

Distribution in space and time of M. nubigens and M. mimosae

The patterns of seed utilization by the two bruchid species appeared to be quite similar. Although data from the dry season of 1987 suggested that *M. mimosae* might attack more *A. farnesiana* green fruits than mature or fallen fruits, the trend did not occur in 1988. Moreover, no preferences for green or mature pods were observed in the laboratory in females of either *Mimosestes* species (unpubl. data). At a larger scale, no segregation was found among shrubs or areas either. When *M. mimosae* was present in a shrub, it always co-occurred with *M. nubigens*; additional laboratory tests showed that there was no preference for pods of a given shrub by either of the two species (unpubl. data).

The relative isolation of plants did not have any effect on intensity of seed predation by any of the species. Plant isolation has been reported in some studies to contribute to a lowered seed predation rate (e.g., Vandermeer 1974); in other studies, however, this pattern has not been found (e.g., Moore 1978; De Steven 1981) or has been found only in interaction with individual plant fecundity (De Steven 1983). If adult bruchids did not fly much among shrubs and stayed near the plant where they were born, isolated plants might suffer a higher intensity of seed predation than plants in clumps. We know nothing about adult bruchid movements but it is unlikely that they stay close to one plant since they feed on pollen and nectar, and these are not always nearby.

Both bruchid species overlapped from the beginning to the end of the season. During both years, *M. nubigens* abundance did not vary through the season while *M. mimosae* was more abundant at the beginning of the fruiting season in 1987, but not in 1988. In general, temporal segregation of bruchid species that attack fruits before they are dropped has rarely been found (Hopkins 1984), since very few species are able to develop in young green fruits (Bridwell 1920; Kingsolver et al. 1977; Hopkins 1983, 1984).

Parasitoids

Urosigalphus sp. was abundant in all areas and throughout the fruiting season, representing 39 and 30% of all insect emergences per shrub in 1987 and 1988, respectively, and reaching up to 70% in some shrubs. Although the frequency of wasps varied among individual plants, it was not associated with any of the plant variables measured.

There is no evidence that *Urosigalphus* sp. distinguishes between the eggs of the two *Mimosestes* species. In the lab, this wasp oviposited equally in eggs laid either by *M. nubigens* or by *M. mimosae* (unpubl. data).

Urosigalphus sp. attacked more bruchid eggs on pods on the shrub than on those beneath it, and their emergences were greater from green than from mature pods. Two, not mutually exclusive, possibilities that might account for this are: (1) the probability of emergence may be higher before the pod valves are too hard (most pods

in which dead adult wasps were found had unusually hard valves), and (2) the bruchid pre-emergence mortality due to heat and desiccation is lower in unripe pods (see next section). Due to their abundance and to their higher number of emergences from green pods, therefore, the parasitoids are favoring those bruchid females that oviposit at a late stage of pod maturation or once the fruits are already on the ground.

Influence of abiotic factors on bruchid survival

Approximately 50% of the bruchid eggs laid on green or mature pods died presumably due to the effect of high temperature and desiccation. Adding this to the loss due to wind blowing away eggs prior to hatching (ca. 30%; Traveset 1990c) it seems likely that abiotic factors provide a major limit to bruchid population growth. Egg survival on fallen pods was also very low (ca. 37%), not significantly lower than at the previous stages, possibly because most eggs are laid on the unexposed valve. High egg mortality in *M. nubigens* presumably due to temperature and desiccation was also reported by Hinckley (1960) in Hawaii.

A large proportion of the larvae that entered the pods died before completing development. More larvae survived to the adult stage in green than in mature or fallen fruits. The high mortality (ca. 50%) inside fallen fruits might be due to the high temperature to which the pods are exposed. There is little air movement at ground level, mainly because of the tall grass around the shrubs, and the soil surface can reach temperatures of 50–70 °C (Janzen 1975a, and pers. obs.).

Beneath the plant, bruchids preferred to oviposit on shaded pods rather than on pods fully exposed to sun. The number of eggs on the "cooler" pods could be almost 10 times the number of seeds they contained. In these cases, there was presumably larval interference inside the seeds, since only one adult can emerge per seed. Cannibalism has been suggested in some species (e.g., Janzen 1971b, 1975b, 1985), although larvae might just kill without eating (Hinckley 1961).

Some species of bruchids are said to minimize larval competition within hosts by accurately assessing the number of eggs on a seed and using this information to produce a near uniform distribution of egg-loads (Wilson 1988 and references therein; Messina and Mitchell 1989). This is certainly not the case here. Regardless of the quantity of fruits available beneath the shrub, the highest number of eggs was observed on "good quality" (fresh, recently fallen, unexposed to direct sunlight) fruits. This suggests that bruchid females are choosing among pods because of the strong selective pressure exerted by harsh abiotic factors. Nevertheless, it is not clear why, in many cases, bruchid females continue to oviposit on the same pod even after all the seeds have been damaged.

Janzen (1975a) also found a high number of bruchid eggs laid on the unexposed valve of fallen pods of *A. far-nesiana*, and suggested that bruchids probably stop ovipositing about the time of pod dropping but continue once pods are on the ground, thereby reducing the probability that a fresh egg is exposed when a pod is dropped. However, plotting the emergence of each bruchid against time passed since the pod was dropped showed that most of the larvae (about 70%) are at a young stage of development when the fruit falls to the ground. Whether the older larvae have a higher probability of surviving the harsh conditions of the environment than the young ones (which have to survive these conditions for a longer period) is unknown, but seems a likely possibility.

High pre-emergence bruchid mortality has also been found in other plants. Mitchell (1977) reported that about 40% of the eggs laid by *Mimosestes amicus* in *Cercidium floridum* were lost to heat and desiccation, and that this made it advantageous for the bruchid female to lay one egg on top of another. Abiotic factors were also probably responsible for the 32% of the bruchid larval mortality observed in the pods of the leguminous *Pithecelobium saman* by Janzen (1977) who reported this mortality as due to unknown reasons. Most pods of this tree are also exposed to sun in the habitats where it lives (pers. obs.). Other causes of larval mortality may be disease, hardness of the endocarp (e.g., Janzen 1971a, b), intense cannibalism and deficient amount of food (e.g., Janzen 1985).

Intensity of seed predation per shrub

The intensity of seed predation varied notably among shrubs, without showing any seasonal pattern. Assuming that adult bruchids move among shrubs and knowing they can live up to 3 months (at least in laboratory conditions, pers. obs.) and have several generations within the 5–6 month fruiting season, an increase in seed predation might be expected during this period. The greatest bruchid mortality appears to be due to the harsh weather conditions, although biotic factors such as parasitism and egg predation by arboreal ants (Traveset 1990c) seem also to be important in reducing population size. Other limiting factors such as predation by birds or microbial diseases may act on the adults. Unfortunately, we know almost nothing about the adult stage of bruchid beetles in nature or about the mortality factors to which they are exposed.

The highest intensity of seed predation in a shrub was about 40%, and much lower values were usual. Apparently, seeds were never in short supply; large proportions of them remained intact despite appearing suitable for bruchid development (not aborted or intensively sucked by hemipterans). Once on the ground, however, the amount of seeds suitable for bruchid oviposition may be substantially reduced depending on local conditions beneath the plant; few seeds within shaded pods survived bruchid predation compared with seeds within exposed pods. Intraspecific competition (especially in *M. nubigens*, since *M. mimosae* appeared to be scarce) might thus occur in shaded pods, limiting bruchid population growth. Nevertheless, this phenomenon should be unimportant compared with the effects of weather and parasitoids.

From an evolutionary perspective, the effects studied here of parasitoids and abiotic factors appeared to exert antagonistic forces, the first selecting for bruchid females that oviposit on already dropped fruits and the second

for those females that oviposit on the hanging fruits. It is perhaps the opposing selection produced by these forces – and probably by others exerted by, for instance, egg predator ants or vertebrate frugivores – that precludes oviposition just on or beneath the shrub. How deterministic the choice by a particular ovipositing female which faces that environmental heterogeneity may be is unknown. This is certainly an aspect that deserves further study.

References

Bridwell JC (1920) Notes on the Bruchidae (Coleoptera) and their parasites in the Hawaiian Islands. Proc Hawaii Entomol Soc 4:403–409

De Steven D (1981) Predispersal seed predation in a tropical shrub (*Mabea occidentalis*, Euphorbiaceae). Biotropica 13:146–150

De Steven D (1983) Reproductive consequences of insect seed predation in *Hammamelis virginiana*. Ecology 64:89–98

Fritz RS, Gaud WS, Sacchi CF, Price PW (1987) Patterns of intra- and interspecific association of gall-forming sawflies in relation to shoot size on their willow host plants. Oecologia 73:159–169

Hartshorn GS (1983) Plants. Introduction. In: Janzen DH (ed), Costa Rican Natural History, Chicago University Press, Chicago, pp 118–157

Hinckley AD (1960) The klu beetle, *Mimosestes sallaei* (Sharp), in Hawaii. Proc Hawaii Entomol Soc 17:260–269

Hinckley AD (1961) Comparative ecology of two beetles established in Hawaii: an anthribid *Araecerus levipennis* and a bruchid *Mimosestes sallaei*. Ecology 42:526–532

Hopkins MJG (1983) Unusual diversities of seed beetles (Coleoptera: Bruchidae) on *Parkia* (Leguminosae: Mimosoideae) in Brazil. Biol J Linn Soc 19:329–338

Hopkins MJG (1984) The seed beetles (Bruchidae) of *Parkia* (Leguminosae: Mimosoideae) in Brazil: strategies of attack. In: Chadwick AC, Sulton SL (eds), Tropical Rain Forest, The Leeds Symposium, Leeds Phil Lit Soc, pp 139–145

Janzen DH (1971a) Seed predation by animals. Ann Rev Ecol Syst 2:465–492

Janzen DH (1971b) The fate of *Scheelea rostrata* fruits beneath the parent tree: predispersal attack by bruchids. Principes 15:89–101

Janzen DH (1975a) Interactions of seeds and their insect predators/parasitoids in a tropical deciduous forest. In: Price PW (ed), Evolutionary strategies of parasitic insects and mites, Plenum Press, New York, pp. 154–186

Janzen DH (1975b) Intra- and interhabitat variations in *Guazuma ulmifolia* (Sterculiaceae) seed predation by *Amblycerus cistelinus* (Bruchidae) in Costa Rica. Ecology 56:1009–1013

Janzen DH (1977) Intensity of predation on *Pithecellobium saman* (Leguminosae) seeds by *Merobruchus columbinus* and *Stator limbatus* (Bruchidae) in Costa Rican deciduous forest. Trop Ecol 18:162–176

Janzen DH (1980) Specificity of seed-attacking beetles in a Costa Rican deciduous forest. J Ecol 68:929–952

Janzen DH (1985) *Spondias mombin* is culturally deprived in megafauna-free forest. J Trop Ecol 1:131–155

Johnson CD (1980) Host preferences of *Stator* in nonhost seeds. Entomol Soc Am 10:857–863

Johnson CD (1981) Interactions between bruchid (Coleoptera) feeding guilds and behavioral patterns of pods of the Leguminosae. Entomol Soc Am 10:249–253

Johnson CD (1983) *Mimosestes playazul*, new species, with new host records for other *Mimosestes* (Coleoptera:Bruchidae). Ann Entomol Soc Am 76:816–820

Johnson CD (1984) New host records and notes on the biology of *Stator* (Coleoptera:Bruchidae). The Coleopt Bull 38:85–90

Johnson CD, Slobodchikoff CN (1979) Coevolution of *Cassia* (Leguminosae) and its seed beetle predators (Bruchidae). Environ Entomol 8:1059–1064

Juliano SM, Lawton JH (1990) The relationship between competition and morphology. II. Experiments on co-occurring dytiscid beetles. J Anim Ecol 59:831–848

Kingsolver JM, Johnson CD, Swier SR, Teran A (1977) *Prosopis* fruits as a resource for invertebrates. Simpson BB (ed), Mesquite, its biology in two desert scrub ecosystems, US/IBP Synthesis series 4, Dowden, Hutchinson & Ross, Stroudsburg, PA, pp 108–122

Lamprey HF, Halevy G, Makacha S (1974) Interactions between *Acacia*, bruchid seed beetles and large herbivores. E Afr Wildl J 12:81–85

Lawton JH, Gaston KJ (1989) Temporal patterns in the herbivorous insects of bracken: a test of community predictability. J Anim Ecol 58:1021–1034

Little EL Jr, Wadsworth FH (1964) Common trees of Puerto Rico and the Virgin Islands. U.S. Dept. Agric., handbook no. 249. Forest Service, Washington

Loreau M (1990) Competition in a carabid beetle community: a field experiment. Oikos 58:25–38

Messina FJ, Mitchell R (1989) Intraspecific variation in the egg-spacing behavior of the seed beetle Callosobruchus maculatus. J Insect Behav 2:727–742

Mitchell R (1977) Bruchid beetles and seed packaging by Palo Verde. Ecology 58:644–551

Moore L (1978) Seed predation in the legume *Crotalaria*. II. Correlates of interplant variability in predation intensity. Oecologia 34:203–223

Pellmyr O (1989) The cost of mutualism: interactions between *Trollius europaeus* and its pollinating parasites. Oecologia 78:53–59

SAS Institute Inc. (1985) SAS User's Guide: Statistics, Version 5 Edition. SAS Institute Inc. Cary, NC

Strong DR, Lawton JH, Southwood R (1984) Insects on Plants. Community Patterns and Mechanisms, Harvard University Press, Cambridge, Mass

Traveset A (1989) Environmental and biological factors affecting the bruchid seed predators of *Acacia farnesiana* (L.) Willd. Dissertation thesis. University of Pennsylvania

Traveset A (1990a) *Ctenosaura similis* Gray (Iguanidae) acting as a seed disperser in a Central American deciduous forest. Am Midl Nat 123:402–404

Traveset A (1990b) Post-dispersal predation of *Acacia farnesiana* seeds by *Stator vachelliae* (Bruchidae) in Central America. Oecologia 84:506–512

Traveset A (1990c) Bruchid egg mortality caused by ants and abiotic factors in the leguminous *Acacia farnesiana* (L.) Willd. Ecol Entomol 15:463–467

Vandermeer JH (1974) Relative isolation and seed predation in *Calliandra grandiflora*, a mimosaceous legume from the highlands of Guatemala. Biotropica 6:267–268

Wilson K (1988) Egg laying decisions by the bean weevil *Callosobruchus maculatus*. Ecol Entomol 13:107–118