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Post-dispersal predation of *Acacia farnesiana* seeds by *Stator vachelliae* (Bruchidae) in Central America

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Summary. Post-dispersal seed predation by the bruchid beetle *Stator vachelliae* was investigated in Santa Rosa National Park, Costa Rica. This insect finds the seeds of the leguminous *Acacia farnesiana* in the feces of horses, deer, and ctenosaur lizards, the current major dispersers. Patterns of oviposition and pre-adult survival of beetles in the seeds were investigated in a series of experiments using fresh horse dung. *S. vachelliae* never minded into the dung balls, attacking only those seeds located on the surface. Fresh horse dung did not attract insects more readily than dry dung. The proportion of seeds attacked was not related to their density in a defecation, and was similar in three areas with different densities of the host plant. In a fourth area with no fruiting *A. farnesiana* shrubs all seeds survived insect predation. Bruchids attacked a greater proportion of seeds at 1 m than at 5 m from the edge of the shrub's crown. Seeds were mainly removed from horse dung by rodents with similar intensity in all areas and at both distances; this seed removal interfered with bruchid oviposition and probably with bruchid survival. *S. vachelliae* oviposited less frequently on seeds in dung fully exposed to sun. When oviposition on a dung pile was high, the distribution of eggs on the seeds was clumped, suggesting that some seeds were preferred to others. By the end of the dry season, bruchids stopped attacking the seeds. The results show that the fate of both seeds and bruchids is greatly influenced by the location and time of defecation.

Key words: *Acacia farnesiana* – Bruchid oviposition patterns – Insect-plant interactions – Post-dispersal seed predation – *Stator vachelliae*

Post-dispersal seed predation studies have demonstrated that frugivorous animals may modify the probability that a seed is found by a seed predator depending upon (1) the distance from a fruiting conspecific at which they disseminate the seeds (e.g., Janzen 1970, 1972; O'Dowd and Hay 1980; Wright 1983; Howe et al. 1985; Webb and Willson 1985; Ramírez and Arroyo 1987; Schupp 1988a), (2) the habitat or microsite where the seeds land (Janzen 1971, 1972, 1982, 1985, 1986; Schupp 1988b; Schupp and Frost 1989), and (3) the local post-dispersal density of seeds (e.g., Wilson and Janzen 1972; Sork and Boucher 1977; Trombulak and Kenagy 1980; Janzen 1982; Ramírez and Arroyo 1987).

Most published information on post-dispersal seed predation has focused on seeds lying on the surface and reports rodents and ants as the predators (e.g., Perry and Fleming 1980; O'Dowd and Hay 1980; Janzen 1982, 1986; Howe et al. 1985; Webb and Willson 1985; Schupp 1988a, b). Much less is known about the patterns of post-dispersal seed predation by insects other than ants (but see Janzen 1971; Wilson and Janzen 1972; Janzen et al. 1976; Janzen 1977; Wright 1983; Howe et al. 1985; Janzen 1985; and Ramírez and Arroyo 1987). Predation on seeds in the feces of animal dispersers has only been studied experimentally for rodents (Janzen 1982, 1986). No equivalent insect data exist.

This study investigates experimentally (1) how seed dispersers of *Acacia farnesiana* (L.) Willd. may influence predation by bruchid beetles on the defecated seeds, and (2) the fate of insects developing within seeds exposed to further predation by vertebrates and to particular environmental conditions. The specific questions addressed were the following: How do (a) density of shrubs of *Acacia farnesiana* in an area, (b) density of seeds in a pile of dung, and (c) distance from the dung pile to the nearest fruiting shrub, affect the intensity of seed attack by bruchids? (d) What is the rate of bruchid oviposition and how are eggs distributed among the seeds in a dung pile? (e) How is the intensity of seed attack affected by the animals that remove seeds from the dung and by environmental agents? and (f) How do the patterns of seed attack by bruchids vary over the season?

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Throughout the paper, the term "intensity of seed attack" is used to mean the proportion of seeds that have bruchid egg(s) on them, regardless of the fate of the developing insect(s). Thus, intensity is only an estimate of the number of seeds preyed upon by bruchids. Moreover, even those seeds in which bruchids have finished development may still germinate if the larvae have not eaten the embryo or most of the cotyledons (Lamprey et al. 1974), even though they will probably not produce a viable seedling.

Study site

The experiments were conducted in Santa Rosa National Park, Guanacaste province, in northwestern Costa Rica, during the dry seasons (January–May) of 1987 and 1988. Santa Rosa consists of about 10800 ha of secondary deciduous forest, with small patches of semievergreen oak forest, and large artificial pastures or savannas on an upland plateau (at 300–350 m elevation). The savannas are dominated by *Hyparrhenia rufa* (Mees.), a grass introduced from Africa in the 1940 s. Clumps of *Acacia farnesiana* are abundant in these artificial grasslands. The climate and vegetation of the area are described in Hartshorn (1983).

Study organisms

Acacia farnesiana (Leguminosae: Mimosoideae) is a shrub or small tree (0.5–5 m tall) native to Central America. It is highly branched and spreading with spines 0.3–10 cm long. The largest trees produce up to about 2000 fruits in a fruiting season. The fruit is an indehiscent brown pod, with thick valves and a sweetish dry pulp, bearing 2–16 hard-coated, ellipsoidal seeds 5–10 mm long. In Santa Rosa, *A. farnesiana* usually flowers from December to March, the fruiting period peaking in the middle of the dry season. Fruiting is asynchronous within and among shrubs. A more extensive account of the plant's life history is given in Traveset (1989a).

The main dispersers of *A. farnesiana* in Santa Rosa are deer (*Odocoileus virginianus* Zimm.), introduced horses (*Equus caballus* L.), and ctenosaurs (*Ctenosaura similis* Gray) (Traveset 1989b). None of these animals, however, appears to have a special preference for the fruits of this plant, and usually a large number of pods accumulate beneath the shrubs. Many of these pods are never dispersed, decaying soon after the first rains arrive by the end of May. Outside Santa Rosa National Park, cattle seem to be the major dispersers of *A. farnesiana* (pers. obs.).

Three species of bruchid beetles prey upon the seeds of *A. farnesiana*, *Stator vachelliae* Bott. being the only post-dispersal predator (Traveset 1989a). In Guanacaste, this bruchid seems to be specific to *A. farnesiana* (Janzen 1980). The female oviposits only on the seeds, either exposed in damaged pods or present in the feces of cows (Johnson 1981), ctenosaurs (Traveset 1989b), and horses (present study). Development takes about 1 month (29–34 days, $N=12$), and several generations may develop per fruiting season. Up to three individuals can finish development in a single seed, although only one or two is usual.

Seeds of *A. farnesiana* in pods or in dung are preyed upon by other animals besides insects. Rodents such as *Sigmodon hispidus* Say & Ord (Cricetidae), common in grasslands, and *Liomys salvini* (Thom.) (Heteromyidae) are presumably the main predators of seeds found in dung. *L. salvini* readily eats the dormant seeds of *A. farnesiana* when it is given several choices in the lab (pers. obs.). Ground-doves (*Columbina* sp.) are often seen pecking horse dung and removing seeds from it. Ants of the genus *Atta* were, on one occassion, seen carrying seeds of *A. farnesiana* and taking only those with a bruchid exit hole (probably lighter and easier to carry).

Material and methods

Experimental dung piles

All dung used in this study came from the population of horses (about 60 individuals) living in Santa Rosa. In 1987 most dung was collected in a large pasture while in 1988 most dung was obtained in the corral. The dung contained mainly grass remains although seeds of *Crescentia alata* HBK. and *Guazuma ulmifolia* Lam. were often present. Seeds of *A. farnesiana* were never observed in the collected dung. All experimental piles consisted of 2 l of moist dung (the average for well-fed adult horses; Janzen 1982) shaped in balls 2–7 cm in diameter and arranged for the experiments 1–3 h after dung was collected. Since the experiments were performed in the dry season, when days are sunny and windy, the horse dung was completely dry after 2–4 days, and no seeds germinated during the whole period. At this time of the year there are no dung beetles (Scarabaeidae) that could disturb the dung (Janzen 1986, and pers. obs.).

Experiment carried out in 1987

The experiment was performed from 11 to 28 March, when most shrubs had started dropping pods. For each pile, I mixed dung and *A. farnesiana* seeds in a plastic bucket, sticking seeds on the surface of the balls and inserting others into them. A screen underneath each pile prevented seed losses at collection. I placed four approximately equal-sized piles of dung, two of low seed density ($n=50$) and two of high seed density ($n=100$), on the ground 1 m from the crown edges of 14 fruiting shrubs, one at each cardinal point. One low-density and one high-density pile (both randomly chosen) around every shrub were covered with a 1-cm mesh metal cate to ensure that at least half of the piles would not be disturbed by rodents. The cage did not affect bruchid oviposition on the seeds (see below). Of the 14 shrubs 10 were in a dense (about 60 indiv./ha) clump of *A. farnesiana* (area 1), while the other four were in a scattered stand 3 km away (area 2, with ca. 30 indiv./ha). This unequal split was due to the difficulty of transporting dung piles to area 2. The experimental dung piles were at least 1 m from the crown edge of any fruiting shrub. The dung was left out for 15 days. I then carefully removed the seeds from the surface of each pile and placed them in small individual plastic bags. All dung was also put in plastic bags for later recovery of unexposed seeds. The dung was soaked in water, completely fragmented, and strained through a 3-mm mesh screen box.

On the day of collection of the experimental dung I recorded the number of bruchid eggs present on the seeds. Bags with seeds were checked every 2–5 days for about a month to record bruchid emergences, and again 2 and 3 weeks later, since in some cases bruchid developmental time is longer when more than one larva develops in a single seed (e.g. Mitchell 1975). The seeds without eggs were also checked since egg shells occasionally fall off after the larvae have entered the seeds.

Experiments carried out in 1988

I placed experimental dung piles in four areas with different densities of *A. farnesiana* shrubs. Areas 1 and 2 were the same as in 1987; area 3, about 500 m from area 1, had about 20 fruiting *A. farnesiana* shrubs in 1 ha, and area 4 was an open pasture with no fruiting shrubs of this species in a diameter of ca. 500 m. Around five shrubs from area 1 and five shrubs from area 3 I placed eight dung piles at compass points, four at 1 m and four at 5 m from the crown edges; 5 m was the maximum distance in the densest area at which I could determine the effect of a single *A. farnesiana* shrub. In area 2 dung piles were placed only at 1 m, to determine whether this year seed attack by bruchids would be as low as in 1987 (see below). In area 4 I placed five dung piles 50 m apart along a line. Since rodents removed almost all seeds from four of the piles in area 4 during the first few days (see below), I replaced those four piles 2 weeks later by new ones. The experiment ran from 24 March to 27 April.

This time, I stuck 50 seeds on the surface only of each pile of dung. I placed no screens to prevent seed removal, and I left the dung for 30 days. Three days after placing the experimental dung piles, I checked all seeds for bruchid eggs to determine if females find the dung more readily when it is still fresh. Seeds were checked again 15 days after dung placement. At each visit to a pile I recorded the number of eggs per seed and the number of seeds present without removing the seeds from the dung balls. After being checked, the dung piles were left as they had been found, intact or disturbed by animals. On day 30, I removed the seeds and recorded the number of eggs on them. As in 1987, I kept the seeds in separate plastic bags to monitor bruchid emergences. I discarded those balls that remained undisturbed, soaking and straining the rest, and checking for any remaining seeds.

Bruchid survival in the seeds

From the 1987 data, I estimated bruchid survival by dividing the number of adult emergences from each pile by the total number of eggs present on the seeds of that pile. In 1988, I observed the eggs under a dissecting microscope to count how many first-instar larvae had entered the seeds; thus, bruchid survival per dung pile at the two different stages (pre- and post-entrance to the seed) was calculated.

Effect of abiotic factors

In 1988, I used a portable lightmeter to estimate the incident radiation on each dung pile. All measurements were recorded between 10:00 and 11:00 a.m. on two consecutive days. The intention was to compare the different dung piles rather than to determine the precise quantity of sunlight reaching each pile.

Influence of time of the season

A new set of 105 pseudodefecations was placed in the field on 5–6 May 1988, just before the rains arrived, at exactly the same locations as in March 1988. I left the dung piles for a month and extracted the seeds exactly as before.

Data analysis

All ANOVAs were executed using the GLM procedure in SAS (SAS 1985). The proportions of seeds attacked were arcsine transformed, and the numbers of seeds removed from the dung piles square root transformed, to normalize the data.

For the 1987 data, I performed chi-square tests (one for each pile bearing bruchid eggs) to compare the observed frequencies of seeds with different numbers of eggs laid on them with the frequencies expected from a Poisson distribution. To determine whether eggs were distributed uniformly or in clumps, I calculated the coefficient of dispersion (Sokal and Rohlf 1981, p. 87) for each pile shown to deviate significantly from the random distribution.

Results

Effect of seed density

Stator vachelliae did not mine into the dung, either fresh or dry, since no seeds within the dung balls were ever attacked. Therefore, intensity of attack by bruchids was considered to be the number of seeds attacked relative to the number of seeds available (i.e., those on the dung surface).

The presence of a cage on half of the piles did not influence seed predation by *S. vachelliae* ($F_{1,9} = 2.51$, $P > 0.05$). A two-way ANOVA with seed density and shrub as the main factors showed that the density of seeds in a pile did not affect significantly the intensity of seed attack by *S. vachelliae* ($F_{1,9} = 1.46$, $P > 0.05$). Shrubs differed significantly in the intensity of seed attack per pile ($F_{9,20} = 7.14$, $P < 0.001$), ranging from 0 to ca. 0.51 ($N = 10$ shrubs). There was no interaction between seed density and shrub ($F_{9,20} = 1.40$, $P > 0.05$).

Only one of the dung piles in area 2 had seeds attacked by bruchids (Table 1), so only the ten shrubs from area 1 were considered in the analyses. The average percentage (±SE) of seeds attacked in area 1 was 24.19% ± 4.67 ($N = 20$ piles) in the low-density piles, and 18.49% ± 4.10 ($N = 20$ piles) in the high-density ones (Table 1).

Effect of area

While dung was fresh, only one pile in the densest area had seeds attacked by *S. vachelliae*. None of the piles in the other areas was located by bruchids. At 15 and 30 days after dung placement, there were no significant differences in the intensity of attack per pile between the densest area (area 1) and the most diffuse one (area 3), either at 1 m from the crown edge ($F_{1,8} = 1.36$ and $F_{1,8} = 1.74$, $P > 0.05$, at days 15 and 30 respectively) or at 5 m from it ($F_{1,8} = 0.33$ and $F_{1,8} = 1.21$, $P > 0.05$) (Table 2). In area 2, where piles were placed only at 1 m from the crown edge, the proportion of seeds attacked per pile was 0.11 ± 0.05 at day 15 and 0.16 ± 0.06 at day 30 ($N = 19$ piles). The intensity of attack per pile varied greatly from shrub to shrub, ranging from 0 to 0.58.18.

The five piles on the savanna without fruiting *A. farnesiana* (area 4) had no seeds attacked by bruchids. Fif-

Table 1. Proportion of seeds attacked (PSA) by bruchids in the dung piles (two of each seed density) placed in 1987, total number of eggs present on the seeds and total number of bruchid adults that emerged from them. The first ten shrubs are from area 1 and the last four from area 2

Shrub #	Seed density	Seeds on surface	PSA	Eggs	Adults
6	50	81	0.24	45	1
	100	132	0.27	65	3
9	50	63	0.34	63	15
	100	109	0.21	53	4
14	50	52	0.06	2	0
	100	85	0.12	13	2
17	50	54	0.45	70	13
	100	112	0.16	36	8
25	50	68	0.44	56	15
	100	112	0.57	182	22
27	50	48	0.02	1	0
	100	87	0.09	11	1
32	50	67	0.17	12	4
	100	89	0.06	10	3
51	50	49	0.55	51	31
	100	99	0.29	78	25
67	50	40	0.16	13	1
	100	82	0.08	7	3
88	50	28	0.00	–	–
	100	78	0.00	–	–
200	50	69	0.00	–	–
	100	94	0.00	–	–
201	50	45	0.00	–	–
	100	80	0.00	–	–
204	50	46	0.00	–	–
	100	118	0.12	20	11
207	50	52	0.00	–	–
	100	107	0.00	–	–

Table 2. Means and standard errors of the proportion of seeds attacked per pile at days 15 and 30 after dung placement in the denset (area 1) and in the most diffuse (area 3) stand of *A. farnesiana* shrubs and at two distances from the crown edges of the shrubs. Data from 1988

Area	Distance (m)	n (piles)	$\bar{x} \pm$SE (15)	$\bar{x} \pm$SE (30)
1	1	20	0.15 ± 0.04	0.26 ± 0.07
	5	19	0.06 ± 0.03	0.08 ± 0.03
3	1	20	0.08 ± 0.03	0.09 ± 0.04
	5	16	0.03 ± 0.02	0.06 ± 0.03

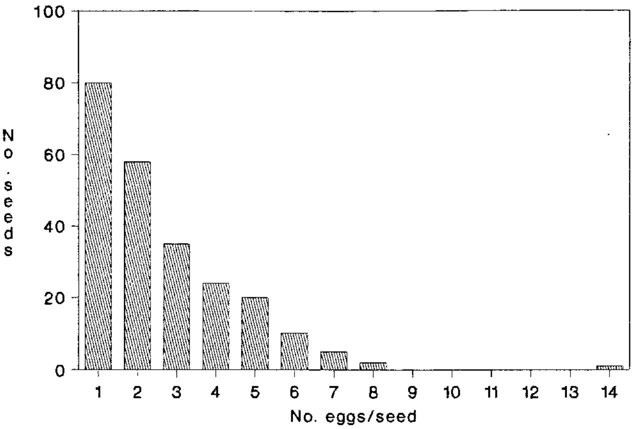

Fig. 1. Distribution of seeds with bruchid eggs present in the 14 dung piles that deviated from a Poisson distribution

teen days after replacing the piles that had been disturbed by rodents, all seeds were present and none of them had eggs. Two weeks later some seeds had been removed, but still none of those remaining was attacked by *S. vachelliae*.

Effect of distance

The probability of a seed being attacked by *S. vachelliae* during the first 15 days of the experiment appeared to be significantly higher ($F_{1,9}=5.35$, $P<0.05$) at 1 m than at 5 m from the crown edge (Table 2). Shrubs differed significantly in the proportion of seeds attacked ($F_{9,55}=3.10$, $P<0.01$) but there was no interaction between shrubs and distance ($P>0.05$).

Fifteen days later, the effect of distance was not significant ($F_{1,9}=3.49$, $P=0.09$), and there was an interaction between shrubs and distance ($F_{9,54}=3.42$, $P<0.01$); in some shrubs the proportion of seeds attacked was still higher at 1 m than at 5 m while in others this difference was not observed.

Five piles located at 5 m, one from area 1 and four from area 3, were shaded by the dense canopies of *Crescentia alata* trees. These piles were not included in the analysis because bruchid oviposition was found to be significantly correlated with sunlight reaching the pile (see below).

Distribution of eggs on the seeds

Of 33 dung piles that had seeds attacked in 1987, 14 exhibited a non-random distribution of eggs on the seeds ($\alpha<0.05$) (Fig. 1); the eggs were laid in clumps (coefficient of dispersion >1). In 12 of those 14 piles there were more than 20 eggs per pile and up to 14 eggs were laid on a single seed. In the remaining 19 piles, the egg distribution on the seeds did not vary significantly from a Poisson distribution ($\alpha>0.05$). The number of eggs in these 19 piles never exceeded 25.

Effect of seed removal

In 1987, an average of 8.0 ± 1.67 seeds per pile ($N=56$ piles) disappeared during the 15 days the dung was in the field. In 1988, seed removal was much greater. While

Table 3. Means and standard errors of the number of seeds removed per pile by days 15 and 30 after dung placement in different areas and at two distances from the crown edges of the shrubs. Fifty seeds were originally present in each pile

Area	Distance (m)	n (piles)	$\bar{x} \pm$SE (15)	$\bar{x} \pm$SE (30)
1	1	20	18.90 ± 3.94	33.10 ± 3.73
	5	20	17.60 ± 3.70	27.55 ± 3.80
2	1	20	20.25 ± 4.44	23.90 ± 4.52
	5	–		
3	1	20	27.00 ± 2.90	35.25 ± 2.51
	5	20	21.00 ± 3.77	28.00 ± 3.39

dung was fresh, 13, 3, and 0 piles were disturbed by rodents from areas 1, 2 and 3, respectively. Seven of the piles from area 1 were located at 1 m from the shrubs and six at 5 m, and rodents removed 15%–90% of the seeds from each pile. After 15 and 30 days of dung placement, the number of seeds removed per pile was similar in those three areas (Table 3), although it differed among shrubs within each area. At day 30 the mean number of seeds missing from each pile around a shrub ranged from 4.50 (9.0%) to 48.25 (96.5%). Distance from a dung pile to a fruiting shrub did not affect the intensity of seed removal ($F_{1,9}=1.54$ and $F_{1,9}=3.02$, $P>0.05$ at days 15 and 30, respectively).

In four of the five dung piles placed in the grassland with no fruiting *A. farnesiana* shrubs, rodents removed 37, 48, 49, and 50 (all) seeds while the dung was still fresh. Fifteen days after replacing those piles there were only 2, 5, 10, and 11 seeds missing from them.

Seeds were removed after having been attacked by bruchids from at least 17 of the total number of dung piles placed in 1988. An average of 29.40% ± 6.00 of the seeds removed from each of these piles between day 15 and day 30 had bruchid eggs on them. The real percentage is probably higher since more seeds might have been attacked and removed before examination. Likewise, a fraction of the seeds removed before day 15 might also have been attacked by bruchids.

Bruchid survival in the seeds

In 1987 the average survival from egg to adult was 25.90% ± 6.90 per pile (range 0–70%, $N=33$ piles). In 1988 that average was 3.05% ± 0.95 (range 0–22%, $N=41$); only 29.84% ± 4.85 ($N=41$) of the eggs on each pile hatched and the larvae entered the seed. Of those larvae, only 13.80% ± 5.10 ($N=28$) became adults. A very small proportion of adults never emerged because they died inside the seed after having made the exit hole.

Bruchid oviposition and survival varied with the light incident on the dung piles. There was a significant correlation between light and (1) number of seeds attacked per pile ($r_S=-0.31$, $P=0.002$ at day 15, and $r_S=-0.30$, $P=0.002$ at day 30, $N=99$ piles), (2) total number of eggs per pile ($r_S=-0.33$, $P<0.001$ at day 15, and $r_S=-0.32$, $P=0.001$ at day 30, $N=100$), (3) number of first instar larvae that entered the seeds ($r_S=-0.30$, $P=0.002$, $N=100$) and (4) number of adult emergences ($r_S=-0.33$, $P<0.001$, $N=100$).

Influence of time of the season

None of the pseudodefecations set out in early May 1988 on the same sites as in March contained seeds attacked by bruchids. Seed removal per pile, however, was as intense as in the middle of the dry season ($F_{1,14}=0.58$, $P>0.05$).

Discussion

The results of the simulated seed dispersal showed how a frugivore may influence the probability of a seed surviving post-dispersal seed predation by beetles, and provided, for the first time, information on the patterns of oviposition by insects on defecated seeds.

The location of a seed in a dung pile was very important in determining the probability of being preyed upon by a bruchid. All those seeds embedded in dung balls survive insect attack simply because the bettle does not dig into them. In natural horse defecations, the number of seeds exposed on the dung surface is presumably usually low, since horses probably eat only small amounts at a time (as with *Enterolobium cyclocarpum* fruits, Janzen 1982). When I fed 50 fruits of *A. farnesiana* (at once) to a horse, the number of seeds defecated in a pile never exceeded 50 during the following 2 weeks over which seeds emerged (unpubl. data). Seeds on the surface of the dung of other dispersers such as ctenosaurs are also attacked by *S. vachelliae* (Traveset 1989b).

Stator vachelliae located dung piles with different densities of *A. farnesiana* with the same probability. This suggests that bruchid females (1) search for seeds once they have encountered a pile rather than looking for seed-rich piles, and (2) find or choose only a fraction of the seeds in each pile encountered.

The fact that *S. vachelliae* attacked a similar proportion of seeds in dung in the three areas where the host plant was present indicates that, all other things being equal, a seed defecated by a horse in a savanna with a high density of *A. farnesiana* shrubs has the same probability of being attacked as another seed defecated in a diffuse stand of the host plant. However, in 1987 seeds were attacked in only one of the 20 piles placed in area 2, suggesting that the local abundance of bruchids may vary annually and/or that the local distribution of bruchids varies among years probably in response to factors other than the presence of fruiting host individuals. On the other hand, in the savanna without fruiting *A. farnesiana* no seeds were attacked by bruchids. This implies that these insects stay in areas where seeds are more likely to be found, either in feces or in damaged pods.

The lower frequency of seed attack by *S. vachelliae* at 5 m compared to 1 m from the crown edge of *A. farnesiana* observed 15 days after dung placement suggests that the bruchids search more intensely below and close to the canopy than a few meters away from it. This is probably because of the higher probability of finding available seeds closer to the plant, as there are always partially opened or damaged pods. A decrease in the intensity of insect seed predation with distance from the parent plant has been reported for other plant species (Janzen 1972; Janzen et al. 1976; Wright 1983; Howe et al. 1985; Ramírez and Arroyo 1987). A month after dung placement distance had no significant effect. This might be because bruchids expand their foraging area when seeds become scarce near the shrub. However, it might also be that rodents removed more seeds with eggs at 1 m than at 5 m between day 15 and day 30.

The effect of distance to a fruiting shrub may not always be as important as the particular conditions of the spot where a dung pile is located. This was suggested by observations of five piles that were placed at 5 m from host shrubs but below dense tree canopies. In the (apparently cooler) conditions of those sites, oviposition on the seeds was intense. Therefore, bruchids might be more abundant not only near the hosts plant but also under nearby shrubs and trees where they might be protected from predators and heat.

When the number of eggs in a dung pile was high, it appeared that the bruchid female(s) had chosen some seeds and oviposited intensely on them rather than evenly distributing their eggs among all seeds. In those piles, there were always seeds without bruchid eggs. The reason why some seeds should be preferred over others is unknown but it might be related to the microsite where the seeds are located on the dung surface. Alternatively, some seeds, just by chance, might not be encountered by the bruchid female(s). Whatever the reason, in these intensely attacked seeds there must be strong competition among sibling or conspecific larvae, since only a maximum of three individuals per seed can complete development. Several studies show that larval competition is reduced by the ability of bruchids to discriminate between seeds with differing eggs loads (e.g., Messina and Renwick 1985; Wilson 1988; Ofuya and Angele 1989); this does not seem to be the case with *Stator vachelliae*.

The animals that remove seeds from the dung have a negative effect on the bruchids by reducing the available resource, and by killing larvae contained in the seeds. A developing larva probably dies when chewed by a rodent (assuming the seed is eaten immediately or soon after being hoarded in a cache or after being carried to a nest), or when crushed in a dove's crop. A minimum of 30% of the seeds removed between days 15 and 30 after dung placement bore bruchid eggs. More seeds might have been attacked and removed during that period. On the other hand, the number of seeds removed was similar at 1 m and 5 m from the crowns of *A. farnesiana* shrubs. In other studies, rodents have been reported to remove more seeds beneath the plants than far from them (O'Dowd and Hay 1980; Herrera 1984; Webb and Willson 1985). Schupp (1988a, b) and Schupp and Frost (1989), however, found that the distance differences depended on the habitat where the seeds were located. The open habitats where *A. farnesiana* is usually found might well explain the failure to find greater removal at 1 m than at 5 m from the shrubs. Even in the densest area, there is much open space between most shrubs.

A striking result was the low bruchid survival inside the seeds during both years of the study, and especially in the dry season of 1988, when an average of only 3% of the eggs laid developed into adults. This high mortality appears to be mainly due to heat and desiccation (ground temperatures can exceed 50° C in April). In those dung piles located under shade or partly shaded by tall grass or branches of nearby shrubs, oviposition on the seeds was more intense, and proportionally more bruchids emerged from them, than in those fully exposed to sun. The reason why bruchid survival was higher in 1987 than in 1988 is not clear but it might be related to the fact that in 1987 the seeds were in the field for a shorter time (15 days); the developing larvae, still at a young stage, might have survived better when taken to the cooler conditions of the laboratory. If this was the case, then bruchid survival is best estimated in 1988 since in this year the dung was left for a month (the average developmental time).

The lack of attacked seeds in the piles placed at the end of the dry season suggests that, by this time, females of *S. vachelliae* no longer search for seeds of *A. farnesiana*, or that there are no longer female bruchids in the area. Although the risk of pre-emergence mortality due to desiccation is now lower, there is the risk of dying in a flooded or rotten seed. As soon as the first rains arrive, many pods and the seeds inside them are covered by fungi (pers. obs.).

In short, a seed of *Acacia farnesiana* dispersed by a horse has a lower probability of being attacked by bruchids when (1) it is embedded within dung balls, (2) it is carried to a grassland where there are few or no *A. farnesiana* shrubs, (3) it is disseminated far from the crown of a host plant, (4) it is defecated in a site exposed to sun, and/or (5) it is dispersed late in the dry season, when *S. vachelliae* no longer oviposits on seeds or is not longer present in the habitat. In turn, a bruchid has a lower probability of survival if (1) the seed it has attacked is removed from the dung before the insect has completed development, and (2) the dung pile with the seed is in a very exposed site.

Seed dispersal seems crucial for the survival of *Acacia farnesiana*. This plant needs open habitats to recruit, and it is precisely in these sites that the dispersed seeds appear less susceptible to attack by bruchids. The experiments reported here suggest that the interaction between frugivores and insect seed predators is more complicated and less predictable than previously thought. In order to understand the dynamics of the ecological triangle comprising plants, seed dispersers, and seed predators in a given system, we need to know more about the influence of environmental and biological factors upon each component of such a triangle.

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