

## Effect of vertebrate frugivores on bruchid beetles that prey on *Acacia farnesiana* seeds

Anna Traveset

Traveset, A. 1992. Effect of vertebrate frugivores on bruchid beetles that prey on *Acacia farnesiana* seeds. – Oikos 63: 200–206.

This study investigated the ecological interactions between the insect seed predators and the vertebrate seed dispersers of the legume *Acacia farnesiana* in Santa Rosa National Park, Guanacaste Province, Costa Rica. The prediction that changes in the disperser populations result in changes in the population of insects, especially in multivoltine species, was tested by simulating frugivores that removed pods with different intensities and at different periodicities. The variables compared were a) number of insects “ingested” and b) number of insects escaped before fruit removal. The data obtained are not the expected from that prediction. A high pre-emergence mortality, due mainly to environmental agents such as high temperatures and desiccation, seems to be responsible for such results.

It is concluded that we cannot easily predict the dynamics of the insect seed predator populations based only in changes in the seed dispersers’ population densities. We first have to determine whether dispersers represent a major factor of insect mortality relative to other factors, biotic and abiotic, that also may limit the insect populations.

A. Traveset, Dept of Biology, Univ. of Pennsylvania, Philadelphia, PA 19104–6018, USA (present address: Inst. d’Estudis Avançats de les Illes Balears, Ctra. de Vallde-mossa, Km 7’5, E-07071 Palma de Mallorca, Spain).

Animal-dispersed plants, frugivorous insects, and seed dispersers may be considered to constitute a complex evolutionary triad in which each component simultaneously interacts with the other two (Herrera 1982, 1984). The relationship between plants and the insects that feed on their fruits (especially those that eat the seeds) has received much attention in the literature (Janzen 1971a, Crawley 1991, and references therein). Likewise, the mutualistic interaction between plants and vertebrate seed dispersers (birds and mammals in particular) has been intensively studied (see reviews by Howe and Smallwood 1982, Estrada and Fleming 1986, Howe 1986, Jordano 1991). In contrast, the third side of the conceptual triangle, namely the interaction between seed dispersers and frugivorous insects, remains poorly known.

Insects may have a negative effect on seed dispersal by making damaged fruits unattractive to birds (Manzur and Courtney 1984, Baver 1986, Burger 1987, Jordano

1987, Knight 1987, Borowicz 1988, Krischik et al. 1989) or mammals (Semel and Andersen 1988).

Alternatively, insects may enhance fruit removal by vertebrates since larvae enrich the nutrient contents of the fruits (Janzen 1971b, Redford et al. 1984, Drew 1988). The reciprocal effect, i.e. that of vertebrates on frugivorous insects, is even less explored (Bigler and Delucchi 1981, Janzen 1982, Herrera 1984, 1989, Drew 1987) and is the one examined here.

By eating the fruits of plants, dispersers (1) decrease the amount of resources available to the insects, and (2) may kill any developing larvae or pupae inside the fruits when these are ingested (cf. Lamprey et al. 1974, Halevy 1974). Presumably, thus, dispersers are selectively favoring those insect females that oviposit early enough in fruit development so that their offspring can leave the fruits before being ingested. This selection has been seen as the result of a “race” (Janzen 1976a) between the dispersers and the insects (the same type of compet-

Accepted 26 September 1991

© OIKOS

itive “race” prop-  
persal agents; Jan-  
predicted that if  
appear or dramati-  
crease in the size  
cially in those sp-  
per fruiting season  
So, for instance,  
cene megafauna  
variety of plants  
a substantial inc-  
predators (Janze-  
(1989) reported  
*Guazuma ulmif-  
to that found in  
Costa Rica, att-  
livestock from  
cidence of seed  
where seed disp-  
Nevertheless,  
resent a major  
relative to othe-  
the population  
translate into  
latter. Some st-  
1987) do sugge-  
jor natural ene-  
which feed on  
predators, how-  
vertebrate fru-  
and in the few  
Halevy 1974,  
factors which  
ered.*

The system  
tuted by *Acac-*  
and its insect s-  
Janzen and M-  
“megafauna s-  
quantities of p-  
being dispers-  
currently “co-  
pothesis that  
have increase  
megafauna di-  
over, we do  
tors prevailed  
tions the syste-  
determine wh-  
in the presen-  
removed the  
quencies, and  
by other bio-  
investigate the  
tebrates wou-  
*A. farnesiana*  
environment  
ined elsewhere

itive "race" proposed later between microbes and dispersal agents; Janzen 1977). Accordingly, it has been predicted that if the major dispersers of a plant disappear or dramatically reduce their populations, an increase in the size of the insect populations results, especially in those species with more than one generation per fruiting season (e.g., Janzen 1971c, 1976a, 1985). So, for instance, the extinction of most of the Pleistocene megafauna – presumably the main dispersers of a variety of plants – in the Neotropics would have caused a substantial increase in the populations of insect seed predators (Janzen and Martin 1982). Recently, Herrera (1989) reported a higher proportion of seeds attacked in *Guazuma ulmifolia* Lam. during 1985 and 1986 relative to that found in 1972 (Janzen 1975) in Palo Verde, Costa Rica, attributing this result to the removal of livestock from the area because no change in the incidence of seed predation was detected in another site where seed dispersers had been present the whole time.

Nevertheless, fruit-eating vertebrates might not represent a major limiting factor of the insect populations, relative to other mortality factors, and thus, changes in the population sizes of the former may not necessarily translate into changes in the population sizes of the latter. Some studies (Bigler and Delucchi 1981, Drew 1987) do suggest that vertebrate frugivores are the major natural enemies of tephritid flies of the genus *Dacus*, which feed on fruit pulp. In the case of insect seed predators, however, there are no data showing that vertebrate frugivores are significant mortality agents, and in the few studies available (Lamprey et al. 1974, Halevy 1974, Herrera 1989), no other biotic or abiotic factors which affect the insect populations are considered.

The system I chose to study this subject is that constituted by *Acacia farnesiana* (L.) Willd., its dispersers and its insect seed predators. This plant is considered by Janzen and Martin (1982) to be an anachronism with a "megafauna syndrome". Indeed, the fact that large quantities of pods accumulate beneath the plant without being dispersed (pers. obs.) suggests that the system is currently "collapsed" (but see Howe 1985). The hypothesis that the insect seed predators of *A. farnesiana* have increased their population sizes since most of the megafauna disappeared is, of course, untestable. Moreover, we do not know what other insect mortality factors prevailed then and in what environmental conditions the system was framed. However, we can certainly determine what would happen to the insect populations, in the present scenario, if we introduced frugivores that removed the fruits with different intensities and frequencies, and compare this influence with that exerted by other biotic and abiotic factors. In this paper I investigate the effect that hypothetical frugivorous vertebrates would have on the bruchid beetles that attack *A. farnesiana*. The effect of factors such as parasitoids, environmental agents and egg-predator ants is examined elsewhere (Traveset 1990a, 1991).

The abundance of this plant in the study area allowed to carry on different experimental manipulations. The manipulations consisted in simulations of different intensities and periodicities of fruit removal – which may represent different frugivore abundances and preferences –, in order to compare (1) the number of insects "ingested" (presumably killed), and (2) the number of insects already emerged before fruit removal. My expectations were that a) the intensity of pod removal would affect bruchid oviposition on the remaining pods, and thus, the number of bruchids emerging from them, and b) the longer the pods remained on or below the shrub without being removed the higher would be the probability of bruchid oviposition and emergence.

## Methods

### Study area

The study was carried out in Santa Rosa National Park, Guanacaste Province, northwestern Costa Rica, during the dry seasons of 1987 and 1988 (preliminary data were gathered in 1986). The area consists primarily of deciduous forest, with small patches of evergreen forest and with large savannas in the upland mesa, at 300–350 m elevation. Santa Rosa used to be a cattle ranch, beginning at least in the early 1800s, and some 30% of its 10800 ha were cleared to pasture. Cattle were removed in 1977–1978. Currently there is a population of horses which, together with fire, help maintaining the pastures. These artificial savannas are dominated by a grass introduced from Africa in the 1940s, *Hyparrhenia rufa* (Mees.).

Santa Rosa receives 1500–2000 mm of annual rainfall from May to December (rainy season). During the rest of the year precipitation and relative humidity are very low. Winds blow strongly the first two months of the dry season (January and February), and the highest temperatures, up to 40°C in the shade, are usually reached in April. A description of the climate and vegetation of the region can be found in Hartshorn (1983).

### Study organisms

*Acacia farnesiana* (Mimosaceae) is a spiny leguminous shrub or tree (0.5–5 m tall), native to Central America, and found at different densities in the grasslands of Santa Rosa. Its bee-pollinated flowers are produced from early December through mid-March. Small green fruits (pods) develop 5–6 wk after fertilization. These fruits require about a month to reach full size and 3–5 wk more to mature. The ripe pods are dark brown, 4–12 cm long and 5–15 mm wide, thick-walled and indehiscent, and contain a sweetish and scented pulp. Inside each fruit there are 2–15 hard-coated seeds which are elliptic, 5–7 mm long. The mature pods remain attached

to the plant for about two or three weeks. Large quantities of pods accumulate underneath the fruiting shrubs throughout the season. A high proportion of these pods is never dispersed and will rot soon after the rainy season arrives. Fruiting is very asynchronous within and among individuals. During the 1987 and 1988 seasons, fruit crop per plant varied from less than 50 to ca. 2000 pods (Traveset 1991).

The current major dispersers of *A. farnesiana* in Santa Rosa are horses (*Equus caballus* L.), white-tailed deer (*Odocoileus virginianus* (Zimm.)), and ctenosaurs (*Ctenosaura similis* Gray) (Traveset 1990b). Outside the Park, cattle eat the fruits of this plant (pers. obs.). Further investigation on where the animals defecate and the fate of the seeds at such places is required to determine the efficacy of these animals as dispersers. The around 60 semi-domestic horses introduced to the Park consume fruits of *A. farnesiana* mostly at the end of the dry season, when fruits of other tree species such as *Guazuma ulmifolia* Lam. and *Enterolobium cyclocarpum* (Jacq.) Griseb. are no longer available. They usually remove fallen pods, but probably take them also directly from the shrub when browsing on the leaves. They do not seem to distinguish intact from insect-damaged fruits. In contrast, native deer are quite abundant in Santa Rosa, although the proportion of pods that they remove from each *A. farnesiana* shrub is apparently low (only occasionally they may remove most of the fruit crop; pers. obs.). It is unknown whether they remove most pods directly from the shrub or from the ground. Deer are frequent at the forest edges, but they are also seen in open grasslands. Captive deer can eat many *A. farnesiana* pods in a short time, the seeds remaining viable after passing through their gut (pers. obs.). *Ctenosaura similis* is an iguanid lizard also native to Central America and common in Santa Rosa. Ctenosaurs have been observed feeding upon fruits only from the ground. Their feces were usually found near shrubs of *A. farnesiana* close to the forest edge, and up to 176 seeds of this plant were counted in a single scat. Seeds are still viable after passing through the lizard's gut (Traveset 1990b).

Two species of bruchids (Bruchidae) feed upon the seeds of *A. farnesiana* before dispersal: *Mimosestes nubigens* (Mots.) and *M. mimosae* (Fabr.). Both have been found as seed predators of other plants (Janzen 1980), but these other hosts are not present in the habitats where *A. farnesiana* is found (pers. obs.). The two species oviposit on full-sized green or mature fruits, and also on fallen pods beneath *A. farnesiana*. Their developmental time is about a month, and only one adult can emerge from a single seed. The fruits become quite dry after approximately two weeks of being shed, and the bruchids stop ovipositing on them. At least in the laboratory, adult bruchids can live several months on a honey diet. A fertilized bruchid female can lay up to 120 eggs (pers. obs.). The bruchids are parasitized by at least five species of hymenopterans, the most com-

mon being *Urosigalphus* sp. (Braconidae) which may attack an average of 30–40% of the bruchids per shrub. The female wasps attack bruchid eggs mostly on hanging pods and very rarely on those laid on fallen ones. A more detailed description of the natural history of the insect seed predators and the parasitoids is in Traveset (1991).

### Experiment performed in the dry season of 1987

The objective was to compare the effect that different sampling plans ("browsing" vs "grazing") would have on bruchid mortality. A total of 57 shrubs were arbitrarily chosen from four savannas (described in Traveset 1989). These shrubs were randomly assigned to one of two groups: one in which only mature fruits would be removed from the branches of the shrub (browsing sampling hereafter) and one in which only fallen fruits would be removed (grazing sampling hereafter). Shrubs assigned to the two groups did not differ significantly in size, crop size or relative position in the habitat. Four treatments combined different periodicities (P, in days) and intensities (I, % of available pods) of removal in each of the two groups: (A) P = 3, I = 20%; (B) P = 3, I = 40%; (C) P = 9, I = 20%; and (D) P = 9, I = 40%. Each shrub was assigned to a single treatment.

I use the terms "browsing" and "grazing" here just to distinguish the two different sampling plans simulated. Most browsers also get food from below the plants (e.g., Baharav 1980), thus the browsing sampling is probably less realistic than the grazing one.

Collections from each shrub began soon after fruits had started being shed. In each visit to a shrub, all mature pods in the branches (for the browsing sampling) and all fallen pods (for the grazing sampling) were counted to calculate the percentage to be removed in that particular shrub. Pods were haphazardly collected and placed inside plastic bags. Once in the laboratory, a maximum sample of 40 pods were kept to monitor bruchid emergences. The number of emergences was taken as the estimate of bruchid mortality due to fruit ingestion by dispersers. The number of bruchids escaped before fruit ingestion was obtained by counting the bruchid exit holes on the pods on the day of collection. Bags were checked every 3–5 d, recording and removing the new emergences. In some cases bruchids mated inside the bags and reoviposited on the pods; however, their offspring emerged much later and were excluded from all analyses.

For each individual plant I recorded fruit crop size, height, and proportion of pods already shed at the time of first collection. Collections started in late March and continued until late April. The number of fruit collections in the experimental shrubs varied among treatments and among individual plants within a treatment, depending on fruit crop size and on the rate at which pods were shed. Collections lasted until all pods had

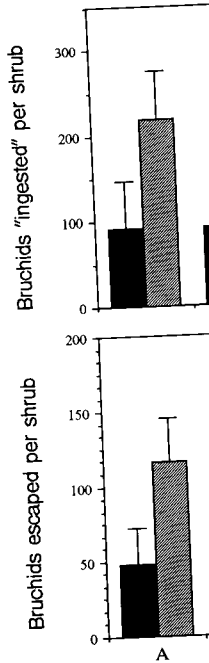


Fig. 1. Number of vertebrate's digestive fruit removal (below) and sampling plans and 20% (n = 9, 7 shrubs) P = 3 I = 40% (n = 9, 7 shrubs) D: P = 9 I = 40% (n = 9, 7 shrubs) shown.

fallen in the shrub until all pods were the grazing sampl

### Experiment pe

The objective th periodicity of fr I haphazardly o them into four shrubs were dif some individual that would visit time intervals counted from continuing until a shrubs. In each ped fruits. Ag were kept to n

Removals s lasted until th

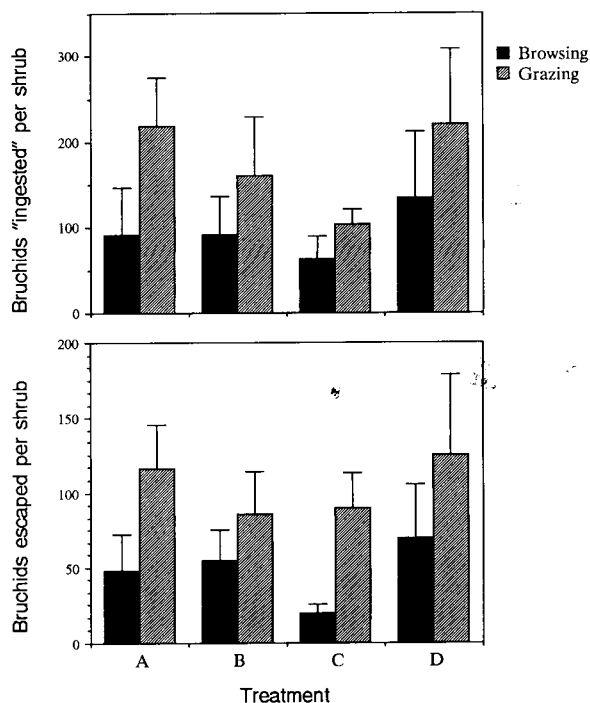


Fig. 1. Number of adult bruchids that would die within the vertebrate's digestive tract (above) and would escape before fruit removal (below), were the dispersers eating fruits at the frequencies (P) and with the intensities (I) simulated in the two sampling plans and in the different treatments. A: P = 3 I = 20% (n = 9,7 shrubs for browsing and grazing, respectively) B: P = 3 I = 40% (n = 6,8), C: P = 9 I = 20% (n = 9,10), and D: P = 9 I = 40% (n = 3,5). One standard error bars are shown.

fallen in the shrubs used in the browsing sampling and until all pods were completely dry in the shrubs used in the grazing sampling.

### Experiment performed in the dry season of 1988

The objective this year was to determine the effect of periodicity of fruit removal alone on bruchid mortality. I haphazardly chose a total of 40 shrubs and divided them into four treatment groups of 10 plants each. The shrubs were different from those used in 1987 except for some individuals. This time I simulated only grazers that would visit the shrubs at different periodicities. The time intervals were: P = 3, 9, 18, and 36 d and were counted from the day the pods had begun falling, continuing until all had been removed from beneath the shrubs. In each visit to a shrub I collected all the dropped fruits. Again, up to 40 pods from each removal were kept to record insect emergences.

Removals started at the beginning of March and lasted until the beginning of May. For each plant I

recorded height, fruit crop size, and period during which pods were dropped. The variables compared among treatments were the same as in 1987.

### Data analysis

All analyses were carried out using the GLM procedure (SAS 1987).

A two-way analysis of variance was performed with the 1987 data, using type of sampling and treatment as main effects. The dependent variables were (1) the number of insects "ingested" per shrub and (2) the number of insects escaped per shrub, both obtained by multiplying the number of bruchids emerged and escaped, respectively, by fruit crop size. From the data gathered in 1988, another analysis of variance was performed to determine the effect of periodicity of fruit removal on the same variables. Logarithmic transformations normalized the data.

Regression analyses were executed with the data from both seasons to estimate the potential influence of the variables measured from each individual plant on the two dependent variables.

## Results

### "Browsing"- "Grazing" comparison

The number of bruchids "ingested" differed significantly between the two types of samplings ( $F_{1,56} = 5.96$ ,  $P < 0.05$ ) but not among treatments ( $F_{3,56} = 0.77$ ,  $P > 0.05$ ) (Fig. 1), and there was no significant interaction between the two factors ( $F_{3,56} = 0.58$ ,  $P > 0.05$ ). Likewise, the number of bruchids emerged before pod removal was higher in the grazing than in the browsing sampling ( $F_{1,56} = 9.77$ ,  $P < 0.01$ ), but did not vary among treatments ( $F_{3,56} = 1.29$ ,  $P > 0.05$ ) (Fig. 1) and, again, the interaction was not significant ( $F_{3,56} = 1.45$ ,  $P > 0.05$ ).

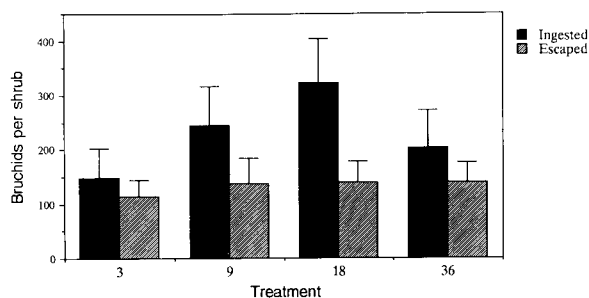


Fig. 2. Number of adult bruchids that a) would die within the vertebrate's digestive tract and b) would escape before fruit removal, were the dispersers eating fruits from below the shrubs at the periodicities (number of days) indicated. n = 10 shrubs per treatment. One standard error bars are shown.

The proportion of pods that had already been shed from a shrub at the time of first collection did not have any influence on the variables of interest here. Fruit crop size was associated with plant height ( $r = 0.37$ ,  $P < 0.01$ ), but this had no relevant effect on either dependent variable ( $P > 0.05$ ).

### Periodicity of fruit removal

The time that pods remained under a shrub did not have any influence either on the number of bruchids "ingested" or on the number of bruchids escaped from that shrub ( $F_{3,39} = 1.72$  and  $F_{3,39} = 0.14$ , respectively,  $P > 0.05$ ) (Fig. 2).

The period during which fruits were being dropped from each shrub was not associated with either fruit crop size or plant height ( $P > 0.05$ ), and did not have a significant effect on any of the dependent variables.

### Discussion

Even though the grazed sample allowed a greater number of bruchids to escape from being ingested than the browsed sample, the former also "killed" significantly more bruchids than the latter. These results were not surprising because most bruchids (70%) in the hanging fruits have not had time to finish development before fruits are shed (Traveset 1991) and because bruchids continue to oviposit on fallen fruits until they are completely dry. The unforeseen results were that neither the intensity nor the periodicity of pod removal from a shrub had a significant effect on the number of bruchids "ingested" or the number of bruchids that escaped before removal.

These unexpected results, however, may be explained if we take into consideration other causes of bruchid mortality. On the shrubs, pods may receive more bruchid eggs the longer they are available; however, those eggs are also exposed for longer to parasitoid wasps (which may kill up to 70% of the bruchids from a single shrub; Traveset 1991), to ants (which may remove an average of about 50% of unhatched bruchid eggs; Traveset 1990a), and to the wind which blows off a high proportion of them (ca. 30%; Traveset 1990a). Likewise, the longer a fallen pod remains uneaten the higher is the probability of being laid on (until they dry completely; Traveset 1991). However, the number of emerging bruchids does not increase significantly with time that pods are beneath the plant because of the great mortality they suffer there. Only about 18% (average for 1987 and 1988) of the eggs laid on dropped pods develop into adults (Traveset 1991). This low survivorship is significantly lower than in pods on the branches, and is attributed mainly to abiotic factors.

During the dry season, the soil surface can reach temperatures between 50 and 70°C (Janzen 1975, and pers. obs.). Most larvae in fallen pods probably die of desiccation, while others may be unable to carve through the hardened seed coat and fruit valve.

On the other hand, if bruchid oviposition was either directly or inversely dependent on fruit density, we might expect the intensity of pod removal to influence the number of bruchid eggs laid on the remaining pods, and thus, the number of bruchids "ingested". However, there appears to be no significant association between number of eggs laid and number of pods available; bruchids rather seem to respond to "quality" (location) of fruits. At least on the ground, bruchid females "prefer" cooler pods located in the shade than hot pods directly exposed to sun. Both oviposition and survival are significantly higher in shady than in sunny fruits (Traveset 1991).

The risk of bruchid pre-emergence mortality probably increases along time that pods are exposed to the harsh conditions of the environment. So, the longer a pod remains on the ground the higher is the probability of being laid on but the lower may be the probability that the eggs will make it to adults. Moreover, a larva that is in a young stage of development when the fruit is shed probably has a lower probability of surviving to adult than an older larva that has to stay under the harsh conditions for only a short period. Even if there was no oviposition on dropped pods, the fact that a large proportion of the larvae has to finish development on the ground may explain why the less frequent pod removals ( $P = 18$  or 36 d) do not present a higher number of bruchid exit holes than the more frequent ones ( $P = 3$  or 9 d).

Bruchid mortality at the larval stage due to heat and desiccation has also been reported in other plants (e.g., Janzen 1975, 1976b, Mitchell 1977), and it is probably more common than previously thought. This is perhaps the reason why intensity of seed predation in some plants (e.g., Janzen 1975, 1985) appears to decline with increasing dryness and exposure of the sites.

Besides physical factors, other causes of bruchid mortality which have been reported for other plants are: microbial diseases, fungi, hardness of the endocarp (Janzen 1971b), intense cannibalism and insufficient amount of food (e.g., Janzen 1985). Unfortunately, we know almost nothing of the adult stage of bruchids. The possibility that the greatest reduction of the insect population sizes occurs at this stage cannot be discarded.

The low frequency with which current dispersers remove fruits from below the plants, the low proportion of pods they eat in each visit to a shrub, and the likely possibility that they remove the most visible ones (those exposed to sun, and thus less attacked by bruchids) indicate that, in the present circumstances, dispersers are killing an irrelevant number of bruchids compared to the other mortality factors. In these extant conditions, only a vertebrate that removed a large proportion

of the fruit crop v  
pods were droppe  
portant effect tha  
and the egg-pred  
ulations. This see  
that existing dur  
habitats where la  
dant, like undist  
fruits of several s  
more than a day  
Halevy 1974). Th  
*farnesiana* in Cer  
grazers were pre  
that in those A  
important role f  
selecting for the  
early stage of fr  
chid oviposition  
*siana* might wel  
of most animals  
speculation, we  
tion patterns of  
acacias in those  
dant.

In areas wh  
hunted out or th  
ically, the pods  
low the plant f  
dorcas gazelles  
1974, Baharav  
stock (e.g., Gw  
Armesto 1981.  
In these depriv  
predators may  
dispersers dep  
biological con

In short, unl  
sent a major m  
tor populations  
density of the f  
density of the  
fruit removal b  
influence of c  
insect populat  
all those facto  
temporal scal  
plants, seed d  
to be rather c  
dispersers, an  
Whether thes  
(coevolutiona  
is a further qu  
of each partic

*Acknowledgem*  
Altaba, B. B. C  
encouragement  
Janzen also com  
design. I am gra

of the fruit crop while still on the shrub, or as soon as pods were dropped, would probably have a more important effect than the physical agents, the parasitoids and the egg-predator ants reducing the bruchid populations. This scenario is probably very different from that existing during the Pleistocene. In contemporary habitats where large herbivorous mammals are abundant, like undisturbed savannas in East Africa, the fruits of several species of *Acacia* do not usually last for more than a day below the shrubs (Lamprey et al. 1974, Halevy 1974). This might well have been the case of *A. farnesiana* in Central America when large browsers and grazers were present (Owen-Smith 1987). It is plausible that in those African habitats the dispersers play an important role limiting the insect population sizes and selecting for those female bruchids that oviposit at an early stage of fruit development. In fact, current bruchid oviposition on mature and fallen fruits of *A. farnesiana* might well have resulted from the disappearance of most animals that ate those fruits. To support such speculation, we would need some data on the oviposition patterns of insects that attack the seeds of African acacias in those habitats where herbivores are still abundant.

In areas where the mammal dispersers have been hunted out or their populations have decreased dramatically, the pods of some *Acacia* species accumulate below the plant for long periods until they are eaten by dorcas gazelles, domestic or wild goats, camels (Halevy 1974, Baharav 1980), ostriches (Baharav 1980), livestock (e.g., Gwyne 1969, Basáñez 1977, Gutiérrez and Armesto 1981, present study), or deer (present study). In these deprived areas, the populations of insect seed predators may or may not be importantly influenced by dispersers depending upon the particular physical and biological conditions present in each area.

In short, unless it is shown that seed dispersers represent a major mortality factor for the insect seed predator populations, we should not expect that a decrease in density of the former will directly result in an increase in density of the latter. Besides evaluating how intense is fruit removal by the vertebrates, we must determine the influence of other factors, biotic and abiotic, on the insect populations, and also consider that the effect of all those factors may notably vary in a spatial and in a temporal scale. The ecological interactions between plants, seed dispersers, and seed predators appear then to be rather complex, as do those between plants, seed dispersers, and microbes (Buchholz and Levey 1990). Whether these interactions translate into evolutionary (coevolutionary, according to these two authors) forces is a further question that requires detailed investigation of each particular situation.

*Acknowledgements* – I am indebted to P. S. Petraitis, C. R. Altaba, B. B. Casper and R. E. Ricklefs for their continuous encouragement and helpful advice during the study. D. H. Janzen also contributed with suggestions on the experimental design. I am grateful to the Servicio de Parques Nacionales de

Costa Rica, especially to F. Cortés, J. A. Salazar and R. Sánchez, for making my stay in Santa Rosa quite pleasant. U. Arieta was very kind in allowing me to feed fruits to deer in his Finca. C. R. Altaba, B. B. Casper, and P. S. Petraitis helped improving an earlier version of this manuscript, the final preparation of which was done at the Estación Biológica de Doñana, Spain. Here I received constructive comments from P. Jordano and C. M. Herrera. I dedicate this work to C. R. Altaba and to U. Chavarría for their kind help in checking pod bags. This paper is part of a PhD thesis performed at the University of Pennsylvania.

## References

- Baharav, D. 1980. Habitat utilization of the dorcas gazelle in a desert saline area. – *J. Arid Environ.* 3: 161–167.
- Basáñez, M. 1977. El huizache, *Acacia pennatula* (Schlecht. & Chan.) Benth. Una invasora del Centro de Veracruz. – *Biótica* 2: 1–18.
- Bauer, G. 1986. Life-history strategy of *Rhagoletis alternata* (Diptera: Trypetidae), a fruit fly operating in a "non-interactive" system. – *J. Anim. Ecol.* 55: 785–794.
- Bigler, F. and Delucchi, V. 1981. Wichtigste Mortalitätsfaktoren während der präpupalen Entwicklung der Olivenfliege, *Dacus oleae* Gmel. (Dipt., Tephritidae) auf Oleaster und kultivierten Oliven in Westkreta, Griechenland. – *Z. ang. Ent.* 92: 343–363.
- Borowicz, V. A. 1988. Do vertebrates reject decaying fruits? An experimental test with *Cornus amomum* fruits. – *Oikos* 53: 74–78.
- Buchholz, R. and Levey, D. J. 1990. The evolutionary triad of microbes, fruits and seed dispersers: an experiment in fruit choice by cedar waxwings, *Bombycilla cedrorum*. – *Oikos* 59: 200–204.
- Burger, A. E. 1987. Fruiting and frugivory of *Cornus canadensis* in boreal forest in Newfoundland. – *Oikos* 49: 3–10.
- Crawley, M. J. 1991. Seed predators and plant population dynamics. In: – Fenner, M. (ed.), *Seeds: the ecology of regeneration in plant communities* (in press).
- Drew, R. A. I. 1987. Reduction in fruit fly (Tephritidae: Dacinae) populations in their endemic rainforest habitat by frugivorous vertebrates. – *Aust. J. Zool.* 35: 283–288.
- 1988. Amino acid increases in fruit infested by fruit flies of the family Tephritidae. – *Zool. J. Linn. Soc.* 93: 107–112.
- Estrada, A. and Fleming, T. H. (eds) 1986. *Frugivores and seed dispersal*. – Junk, Dordrecht.
- Gutiérrez, J. R. and Armesto, J. J. 1981. El rol del ganado en la dispersión de las semillas de *Acacia caven* (Leguminosae). – *Ciencia Invest. Agrar.* 8: 3–8.
- Gwyne, M. D. 1969. The nutritive values of *Acacia* pods in relation to *Acacia* seed distribution by ungulates. – *E. Afr. Wild. J.* 7: 176–178.
- Halevy, G. 1974. Effects of gazelles and seed beetles (Bruchidae) on germination and establishment of *Acacia* species. – *Israel J. Bot.* 23: 120–126.
- Hartshorn, G. S. 1983. *Plants. Introduction*. – In: Janzen, D. H. (ed.), *Costa Rican Natural history*. Chicago Univ. Press, Chicago, pp. 118–157.
- Herrera, C. M. 1982. Defense of ripe fruit from pests: its significance in relation to plant-disperser interactions. – *Am. Nat.* 120: 218–241.
- 1984. Avian interference of insect frugivory: an exploration into the plant-bird-fruit pest evolutionary triad. – *Oikos* 42: 203–210.
- 1989. Vertebrate frugivores and their interaction with fruit predators: supporting evidence from a Costa Rican dry forest. – *Oikos* 54: 185–188.
- Howe, H. F. 1985. Gomphothere fruits: a critique. – *Am. Nat.* 125: 853–865.
- 1986. Seed dispersal by fruit-eating birds and mammals. –

- In: Murray, D. R. (ed.), Seed dispersal. Academic Press, North Ryde, Australia, pp. 123-190.
- and Smallwood, J. 1982. Ecology of seed dispersal. - Ann. Rev. Ecol. Syst. 13: 201-228.
  - Janzen, D. H. 1971a. Seed predation by animals. - Ann. Rev. Ecol. Syst. 2: 465-492.
  - 1971b. The fate of *Scheelea rostrata* fruits beneath the parent tree: predispersal attack by bruchids. - *Prineipes* 15: 89-101.
  - 1971c. Escape of *Cassia grandis* L. beans from predators in time and space. - *Ecology* 52: 963-979.
  - 1975. Intra- and interhabitat variations in *Guazuma ulmifolia* (Sterculiaceae) seed predation by *Amblycerus cistelinus* (Bruchidae) in Costa Rica. - *Ecology* 56: 1009-1013.
  - 1976a. Two patterns of pre-dispersal seed predation by insects on Central American deciduous forest trees. - In: Burley, J. and Styles, B. T. (eds), Tropical trees. Variation, breeding and conservation. Linn. Soc. Symp. Ser. 2, pp. 179-188.
  - 1976b. Two Costa Rican bat-generated seed shadows of *Andira inermis* (Leguminosae). - *Ecology* 57: 1068-1075.
  - 1977. Why fruits rot, seeds mold, and meat spoils. - *Am. Nat.* 111: 691-713.
  - 1980. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. - *J. Ecol.* 68: 929-952.
  - 1982. Simulation of *Andira* fruit pulp removal by bats reduces seed predation by *Cleogonus* weevils. - *Brenesia* 20: 165-170.
  - 1985. *Spondias mombin* is culturally deprived in megafauna-free forest. - *J. Trop. Ecol.* 1: 131-155.
  - and Martin, P. S. 1982. Neotropical anachronisms: the fruits the Gomphotheres ate. - *Science* 215: 19-27.
  - Jordano, P. 1987. Avian fruit removal: effects of fruit variation, crop size, and insect damage. - *Ecology* 68: 1711-1723.
  - 1991. Fruits and frugivory. - In: Fenner, M. (ed.), Seeds: the ecology of regeneration in plant communities (in press).
  - Knight, R. S. 1987. Coping with seed parasitism: a possible response by *Protasparagus aethiopicus*. - *Oikos* 48: 15-22.
  - Krischik, V., McCloud, E. S. and Davidson, J. A. 1989. Selective avoidance by vertebrate frugivores of green holly berries infested with a cecidomyiid fly (Diptera: Cecidomyiidae). - *Am. Midl. Nat.* 121: 350-354.
  - Lamprey, H. F., Halevy, G. and Makacha, S. 1974. Interactions between *Acacia*, bruchid seed beetles and large herbivores. - *E. Afr. Wildl. J.* 12: 81-85.
  - Manzur, M. I. and Courtney, S. P. 1984. Influence of insect damage in fruits of hawthorn on bird foraging and seed dispersal. - *Oikos* 43: 265-270.
  - Mitchell, R. 1975. The evolution of oviposition tactics in the bean weevil *Callosobruchus maculatus* (F.). - *Ecology* 56: 696-702.
  - Owen-Smith, N. 1987. Pleistocene extinctions: the pivotal role of megaherbivores. - *Paleobiology* 13: 351-362.
  - Redford, K. H., Da Fonseca, G. A. B. and Lacher, T. E. 1984. The relationship between frugivory and insectivory in primates. - *Primates* 25: 433-440.
  - SAS Institute Inc. SAS/STAT Guide for Personal Computers, Version 6 Edition. - Cary, NC: SAS Institute Inc., 1987.
  - Semel, B. and Andersen, D. C. 1988. Vulnerability of acorn weevils (Coleoptera: Curculionidae) and attractiveness of weevils and infested *Quercus alba* acorns to *Peromyscus leucopus* and *Blarina brevicauda*. - *Am. Midl. Nat.* 119: 385-393.
  - Traveset, A. 1989. Environmental and biological factors affecting the bruchid seed predators of *Acacia farnesiana* (L.) Willd. - Ph.D. thesis, Univ. of Pennsylvania.
  - 1990a. Bruchid egg mortality caused by ants and abiotic factors in *Acacia farnesiana* (L.) Willd. - *Ecol. Ent.* 15: 463-467.
  - 1990b. *Ctenosaura similis* Gray (Iguanidae) acting as a seed disperser in a Central American deciduous forest. - *Am. Midl. Nat.* 123: 402-404.
  - 1991. Pre-dispersal seed predation in Central American *Acacia farnesiana*: factors affecting the abundance of co-occurring bruchid beetles. - *Oecologia* 87: 570-576.