

## SPECIFICITY OF SEED-ATTACKING BEETLES IN A COSTA RICAN DECIDUOUS FOREST

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### SUMMARY

(1) The deciduous forests and the riparian evergreen vegetation that they include in the lowlands of Guanacaste Province, Costa Rica, contain at least 975 species of dicotyledonous plants. At least 110 species of beetles (Coleoptera) whose larvae are seed-predators were reared from more than 3700 samples of fruits and seeds of these plants.

(2) At least 100 species of these plants usually had beetle seed-predators (Bruchidae, Curculionidae, Cerambycidae) in their mature or nearly mature fruits or seeds.

(3) Most (75%) of the species of beetles were specific to a particular plant species; 14 preyed on two plant species, 9 on three, and 2 on four. The bruchid *Stator pruininus* preyed on six species and *S. limbatus* on eight species.

(4) Of the 100 species of plants whose seeds were preyed on regularly by beetles, 63 were in the Leguminosae, 11 in the Convolvulaceae, and the remainder were spread among sixteen other plant families.

(5) Of these 100 prey species, 59 were fed on by a single species of beetle, 25 by two species of beetles, 11 by three, 4 by four and one, *Cassia leptocarpa*, by five species of beetles.

(6) In at least 90% of seed or fruit samples, all species of beetles attacking that species in the study area were present. Of the 100 species of beetles, eighty were found in the first sample of the appropriate fruit or seeds. The prey of ten additional species of Bruchidae in the study area is unknown, but will be other than the prey species listed here.

(7) With some striking exceptions, the prey species of those beetle species which preyed on more than one plant species were closely related. In contrast, in those cases where there were two or more congeneric plant species in the study area, the species of beetle which attacked one or more of them left unattacked an average of 5.8 of the congeneric plant species.

(8) There were five unambiguous cases of a prey species that occurred throughout the study area and that had two or more species of beetle seed-predator whose distributions did not overlap at all.

(9) Hymenopterous parasitoids were uncommon in most of the samples and were absent from large samples of a number of common tree species whose seeds were heavily preyed on by beetles. Of the 157 predator-prey pairs reported here, 57% of the beetle species were unattacked by hymenopterous parasitoids.

(10) The distribution of beetle predator species among the plant prey-species was conspicuously neither random nor uniform. Unexpectedly large numbers of species were either unattacked, or preyed on by two to five species of beetles, while unexpectedly small numbers were attacked by a single species of beetle.

(11) The prey-specificity of most of these seed-predators in a species-rich flora is of great importance in understanding the potential impact of animals on plant species-richness, but is not proof that seed predation by animals *causes* extreme plant

species-richness. Furthermore, these beetles are only a small fraction of the animals that kill or weaken plants in a manner that may influence their abundance and spatial distribution.

## INTRODUCTION

In a tropical forest rich in plant species, how specific are the seed-predators? This paper records the results of rearing Coleoptera (beetles) from field-collected samples of seeds and fruits from the lowland deciduous forests on the Pacific coast of Costa Rica since 1965. These results bear on, but do not test, the hypothesis (Janzen 1970) that animals influence plant species-richness. The results show that in contrast with carnivorous predators, seed predators are strikingly prey-specific. This study is concerned *only* with those beetle seed-predators that live inside the fruit or seed between the time it approaches full size and the time it is dispersed. Some generalizations from this study have been used in work already published (Janzen 1973a, 1974a, 1975a, 1976a, 1977a) but this report supersedes these accounts.

## THE STUDY AREA

The study area is Guanacaste Province below about 400 m elevation and excluding the Nicoya Peninsula. The area is about 160 km long and 15–30 km wide (about 3200 km<sup>2</sup>), bounded to the west by the sea and the Golfo de Nicoya, and by the remains of the deciduous forest at the base of the Nicoya peninsula, and to the east by mountains clothed in evergreen forest.

The mean monthly temperature is about 28 °C, with a fluctuation in the mean from month to month of little more than 2 °C. The annual rainfall in the study area varies with place and year from 900 to 2500 mm. At least 99% of the rain falls between mid-May and mid-December, and there is often a conspicuous second short dry-season (*veranillo*) of 1–4 weeks duration between late-June and mid-August. In the forest that once covered the study area, the majority of the species of trees away from watercourses and marshes were leafless during much of the long dry season, especially on hillsides that face directly into the strong northeast dry-season trade-winds. In the moister habitats (about 2% of the study area), many species were evergreen but others were leafless for several months. This deciduous forest, with its contained moister habitats, had about 975 species of dicotyledonous plants, about 70% of which were woody perennials (Opler 1980; Janzen & Liesner 1980). About 90% of the forest has now been cleared or is in various stages of regeneration. Its plants and animals are still present, but in highly altered densities and distributions, except in the Parks and reserves where most of this study was conducted. Other information about the study area and its weather and physical conditions is given by Janzen (1967, 1973b, c, 1976b, c); Daubenmire (1972); Frankie, Baker & Opler (1974); Heithaus, Fleming & Opler (1975) and Glander (1978).

## METHODS

### *Beetle biology and rearing*

The female of a typical beetle seed-predator (Bruchidae, Curculionidae, Cerambycidae) lays one or a few eggs on or in the surface of a full-sized and nearly mature fruit. Each female lays 50–100 eggs in her lifetime. She only rarely moves from the fruit crop in the

crown of a large tree to that in another well-separated tree. Patches of small plants are treated as if they were one large tree crown. A first instar larva bores through the fruit wall and then into the seed (which often still has a soft seed coat). The larva eats the contents of the seed and pupates there 2–4 weeks after the egg hatched. The adult emerges 1–3 weeks later, shortly before the seeds or fruits are dispersed, and lives free, visiting flowers for nectar and pollen, until the next fruit crop of its prey species is susceptible (usually an 8–10 month wait). About 30% of the beetle species found as seed-predators show significant deviations from this pattern. Some larvae move from seed to seed within the fruit, some species have several generations per year on prey populations with a long period of fruit availability, and some lay their eggs on dispersed seeds or nuts.

Beetles were reared from large samples of ripe or nearly ripe seeds or fruits. These were tightly packed into a thin-walled plastic bag which was tied shut and then hung inside a large inflated and closed plastic bag. Both were hung from a ceiling at outdoor temperatures for several months. When the beetles and their parasitoids emerged, they commonly cut exit holes through the first plastic bag but then lived their lives walking about the inflated plastic bag. In some cases this technique had to be modified. Moist fruits or seeds, which might be attacked by fungi, were put in open-mesh bags or cardboard boxes, rather than plastic bags. Many species of weevils (Curculionidae) pupate in soil, so the larvae of these species were collected from the bottoms of the bags and put onto soil in small bottles. The adults emerged several weeks to months later. Newly hatched individuals of some species of bruchids (especially in the genera *Acatoscelides*, *Mimosestes*, *Stator*, and *Zabrotes*) oviposited on the dry seeds or fruits in the bag and so produced second or even third generations of predators in the sample. Samples of this kind were not used to determine the intensity of predation. Moth larvae (often Pyralidae) boring through fruits were a constant nuisance. They consumed seed fragments left by beetle larvae and sometimes, falsely, appeared to be seed-predators (though some of them actually are seed-predators). They were avoided by collecting clean fruit, and sufficient samples were taken so that some were moth-free by chance.

Contaminants were an omnipresent problem: field-collected samples occasionally contained adult beetles of species that never prey on the species of seed in the sample. For example, a large cluster of dry *Triplaris melaenodendron* fruits, a species with no pre-dispersal beetle seed-predators, had six species of adult bruchids hidden in it. Such contaminants were avoided by careful collection of intact fruits, by working out the natural history of each species of beetle, and by rearing from isolated fruits and seeds. It was more difficult to deal with the occasional beetle that developed to maturity in the seeds of a species on which it normally does not prey. Because of the large number of samples and the consistent results from them, some unusual records are suspect. They have been omitted from the main results, but are listed separately.

#### Taxonomy

The plant names follow Janzen & Liesner's (1980) checklist of lowland Guanacaste plants. In three cases the names are different from those used in other recent papers on the biology of Guanacaste plants: new *Pterocarpus rohrri* = old *P. hayesii*, *Guazuma ulmifolia* = *G. tomentosa*, *Manilkara zapota* = *Achras zapota*. Vouchers for all plant species are in the herbarium of the Missouri Botanical Garden. There is probably only one population of plants in Guanacaste for each of the names used, except that '*Piptadenia flava*' may be two species with very similar fruits. The samples of seeds of *Spondias mombin* and *S. radlkoferi* were not differentiated, but this does not affect the calculations,

as *Amblycerus spondiae* occurs in all samples from both species of tree in the southern part of the study area.

Beetle names follow the references in Appendix 1. Some of these names may include more than one population. For example, individuals of *Megacerus cubicus* preying on *Ipomoea carnea* had about twice the body volume of *Megacerus cubicus* reared from *Ipomoea nil* seeds.

Voucher specimens of all the beetles in this study are in the Kingsolver collection of Bruchidae at the U.S. National Museum, Washington.

#### *Seed and fruit sampling*

Samples of seeds and fruits were collected from plants growing in conditions ranging from isolated trees or herbs in open pastures to plants in largely intact forest. The intact forests are in Santa Rosa National Park (referred to hereafter as SRNP) which is about 40 km south of Peñas Blancas on the Nicaraguan border (10°45' to 11°00'N latitude, 85°30' to 85°45'W longitude) and in the COMELCO ranch near Bagaces (see Frankie, Baker & Opler 1974 for description). Numerous rearings were also made from seeds collected to the south in the drier northern portions of Puntarenas Province, but these are included here only if the plant and insect relationship extends well into Guanacaste Province.

The goal was to discover all the species of insects that prey on seed crops in the study area. Since habitat destruction around a plant generally increases the probability that one or more of its seed-predators will be missing or greatly reduced in density (e.g., Janzen 1971a, 1974b, 1978a), a special effort was made to sample seed crops in vegetation undisturbed by man as well as in farm- and pasture-land. None of the results suggested that the prey-specificity reported here differs qualitatively from that before the vegetation of Guanacaste was modified by human activities.

Samples of seeds and fruits were generally collected directly from the parent plant or from the ground below it. Usually these samples contained fruits or seeds ready or nearly ready for dispersal, but immature samples believed to be free of insects were examined by dissection and by storing for potential insect emergence. I continued to collect samples until no new species of insects appeared, and dissected or examined many samples in the field to substantiate this conclusion.

By the end of the 13-yr study more than 3700 samples from more than 90% of the woody plants and at least 60% of the herbs had been examined, including more than 1100 samples from species that had no beetle seed-predators. Almost all of the unsampled herbs have very small seeds of a size that would usually be taken by granivorous birds, lygaeid bugs or other non-beetle seed-predators.

Bruchidae are by far the largest taxon of beetle seed-predator in the study area and, of the Coleoptera, kill the most seeds. Ten species which were not reared from seeds were found by general collecting. Their prey remains unknown, and they may even be transients in the study area. A few species of beetle oviposit on seeds only after seed dispersal and some of these may have been missed. Those beetle species that prey on a particular species of seed usually find almost all the seed crops of that species. Exceptions are those cases where the seed crop may come from a plant in a barren and disturbed habitat, from a part of the study area that is outside the range of the insect, or from a time of year during which the plants do not normally bear susceptible fruits.

In short, the large number of samples examined, the high proportion of the flora sampled, the small number of seed-predators discovered by other forms of collecting, and

the efficiency with which beetles locate their prey all indicate that the results, if not comprehensive, are so nearly so that reliable conclusions may be drawn.

Some species have been omitted, however. The following qualifications concern them.

(1) Some species of weevils (Curculionidae) reared at very low density from fruit and seed samples may also feed as larvae in galls, flowers, stems or fruit pulp. Their natural history is so poorly known that they have been excluded. Some examples of such weevils are *Apion sublaterale* Kissinger in seeds of *Lonchocarpus* Boucher 544, *Chrysapion chryso-comum* (Gerstaecker) in seeds of *Aeschynomene americana*, and other weevils in seeds of *Dalbergia glabra* and *Lonchocarpus costaricensis*.

(2) In addition, some species of plants listed in Appendix 1 are attacked, rarely, by weevils or moth larvae which have not yet been successfully reared or identified. Some examples are *Caesalpinia eriostachys*, *C. exostemma*, *Canavalia brasiliensis*, *Desmanthus virgatus*, *Gliricidia sepium*, *Lonchocarpus acuminatus*, and *Machaerium arboreum*.

(3) The larvae of a number of species of moths destroy fruits rather than their contained seeds (e.g. the pyralid moths that feed on the fruits of *Cassia grandis*, *Cordia dentata*, *Enterolobium cyclocarpum*, *Guazuma ulmifolia* and *Pithecellobium saman*). These animals may have the same effect as seed-predators if they deter seed-dispersing animals from eating the fruits (Janzen 1977e) but have been omitted.

(4) The seeds of some plant species, for example *Albizzia caribaea*, *Calliandra costaricensis*, *Crotalaria* spp., *Lysiloma seemanii*, *Psittacanthus calyculatus*, and *Quercus oleoides* are commonly attacked by moth larvae, but moths are omitted.

(5) Several species of anobiid beetles (adults and larvae of *Tricorynus* spp.) feed regularly on the fruits and seeds of the plant species listed in Appendix 1 (e.g. *Hymenaea courbaril*, *Guazuma ulmifolia*, *Lonchocarpus rugosus*, *Pisonia macranthocarpa*, *Pithecellobium saman*, etc.), but the taxonomic distinction between species is very small (White 1965, 1967). No taxonomist able to make these distinctions was available, so these species are omitted.

(6) Introduced plants, even though preyed on by indigenous beetles, are omitted. Many such plant species (e.g. *Caesalpinia pulcherrima*, *Delonix regia*, *Tamarindus indica*) have seeds large enough for beetle larval development, but only *Cassia alata* (a scarce legume shrub) is attacked. Of eleven samples of this species, three produced numerous *Amblycerus obscurus*, and two produced numerous *Sennius instabilis*. Both of these bruchids are common on other sympatric species of *Cassia* with similar woody semi-indehiscent fruits.

(7) In rare cases the beetles make mistakes. In one case nuts and seeds were collected from howler monkey faeces (by C.R. Carroll). Of 197 *Spondias mombin* nuts, more than 40% had eggs of *Amblycerus spondiae* (the usual seed-predator) attached and in due course a single adult emerged from each. Of 331 *Eugenia salmensis* seeds in the same sample, six had an egg of *A. spondiae* attached and later a single adult emerged from each. Thousands of other *E. salmensis* seeds have shown no sign of bruchid attack. It seems probable that the beetle was misled in this case by the smell of *S. mombin* fruit that was strong in the monkey faeces. This record has been omitted.

Three further qualifications must be made.

(8) The proportion of the samples containing a seed-predator and the intensity of seed predation by that predator depend on the developmental stage of the fruit and seed when it was collected, as well as on the habitat of the parent plant. For example, the ripe fruits of *Scheelea rostrata* and *Spondias mombin* have no bruchids in their nuts until the fruit pulp has been removed from the fallen nut and the bruchid has had time to oviposit on it (Janzen 1971a; Wilson & Janzen 1972). If intact *Cassia grandis* pods are collected before

*Pygiopachymerus lineola* adults have emerged, the sample never contains *Stator interstitialis* because this small beetle can enter the indehiscent pods only through the exit holes of *P. lineola* (Janzen 1971c). I have reported on the intensity of seed predation in the study area in single-species accounts (Janzen 1971a, b, c, 1972, 1975a, b, c, 1977b, 1978a, b; Janzen *et al* 1976; Wilson & Janzen 1972) and others report similar work in other New World habitats (Johnson & Kingsolver 1975; Baskin & Baskin 1977; Johnson 1977a, b, c, 1977d; Mitchell 1977).

(9) Calculations using the results in Appendix 1 are complicated by the fact that in five cases, the seeds of a single plant species are preyed on by two or more allopatric species of beetle that are both common within the study area (*Centrosema pubescens*, *Ipomoea carnea*, *Mimosa pigra*, *Pterocarpus rohrii* and *Rhynchosia minima*). The statements that *Ipomoea carnea* is preyed on by three species of *Megacerus* and that *Cassia biflora* is preyed on by three species of bruchid have different implications. *Ipomoea carnea* is preyed on by two species at one site (SRNP) and a single (different) species at another (Palo Verde National Park at COMELCO), but *C. biflora* is preyed on by the same three species throughout much of the study area. In these five cases, I have chosen to treat each of the prey subpopulations of a single plant species as a separate entity. Therefore, although there are ninety-five prey Latin names listed in Appendix 1, they are treated throughout this paper as 100 'species'. This manipulation would not be required were the study area but a few kilometres across.

(10) The comments that follow apply to the study area alone. Thus *Megacerus maculiventris* preys only on *Ipomoea nil* in the study area but *M. maculiventris* has been reared from at least four other species of the Convolvulaceae in the neotropics (Teran & Kingsolver 1977).

## RESULTS

The main results are shown in Appendix 1 and cases suspected of being contaminants in Appendix 2.

### *Specificity of predator and prey*

There are 110 species of beetle seed-predators listed in Appendix 1, and 100 'species' of plants. Of the beetles, 83 species have only one prey species, 14 have two, 9 species have three and 2 species have four species of prey. *Stator pruininus* has six and *S. limbatus* has the most with eight species of prey. These two species of *Stator* have no prey species in common in the study area. Among the weevils (Curculionidae), *Phymatophosus scapularis* has two prey species but the other 11 species have only one prey species each. All three species of Cerambycidae have only one prey species each. The extreme prey-specificity summarized here is especially noteworthy because the study area contains at least 975 species of dicotyledonous plants.

Of the 100 plant species whose seeds are preyed on by the beetles, 63% belong to the Leguminosae and 11% to the Convolvulaceae, but only 17% of the plant species in the study area belong to the Leguminosae and 3% to the Convolvulaceae. The remaining 26% of potential prey species are distributed as follows: Boraginaceae 4%, and 1% each in Palmae, Combretaceae, Ebenaceae, Sapotaceae, Vitaceae, Flacourtiaceae, Tiliaceae, Sterculiaceae, Euphorbiaceae and Bixaceae. All ten of the records of attacks on the Convolvulaceae are of *Megacerus*, a distinctive genus of moderately brightly coloured bruchids that prey only on seeds of Convolvulaceae (Teran & Kingsolver 1977), and

eleven are of *Amblycerus*, a distinctive genus of large drab bruchids that attacks many plant families throughout the neotropics (Kingsolver 1970c, 1980b). All three of the Cerambycidae records are from seeds of non-legume families, as are five of the twelve weevil (Curculionidae) records. Viewed the other way around, Appendix 1 shows that in addition to *Megacerus* being restricted to the Convolvulaceae, *Sennius* is largely restricted to preying on *Cassia* (Johnson & Kingsolver 1973), *Ctenocolum* to fabaceous legumes closely related to *Lonchocarpus* (Kingsolver & Whitehead 1974a), and *Merobruchus* to mimosaceae legumes closely related to *Lysiloma*.

Of the 100 prey 'species', 59 have only one species of beetle feeding on the seeds, 25 have two, 11 have three, 4 of the prey have four predators, and one (*Cassia leptocarpa*) has five. Of the other 4 species with a large beetle fauna (*Albizzia caribaea*, *Andira inermis*, *Piptadenia flava*, *Prosopis juliflora*), '*P. flava*' may perhaps be two species of plants as there is no case where all four seed predators occurred in one sample. The species in the genera *Acacia*, *Albizzia*, *Cassia*, *Lonchocarpus* and *Mimosa* are noteworthy for having no or else more than one beetle species feeding on their seeds.

The small number of beetle species per prey species is not a mandatory result of high prey-specificity: if there were more species of beetles and the same specificity then the average number of beetles per prey species might be higher.

In most cases where a beetle preys on more than one species of seed, the set of attacked species are closely related (Appendix 1, column 2.) The four major exceptions are: *Amblycerus spondiae* on *Spondias* (Anacardiaceae) and *Hippomane* (Euphorbiaceae); *Mimosestes amicus* on *Prosopis* (Mimosoideae) and *Parkinsonia*; *Mimosestes mimosae* on two species of *Acacia* (Mimosoideae) and on *Parkinsonia* and *Caesalpinia* (Caesalpinioideae); *Stator pruininus* on *Sesbania* (Caesalpinioideae) and *Mimosa* and *Desmanthus* (Mimosoideae). However, a given beetle species often does not prey on all closely related species of plants in the habitat. In column 9 of Appendix 1 are recorded the number of congeneric species that are not preyed on for each of the predator-prey pairs, where there is more than one species in the same genus in the study area. There are ninety such cases. In these cases, the beetle does *not* prey on the seeds of an average of 5.8 species that are congeneric with its prey species (S.D. = 4.6). The most extreme cases are the species of *Amblycerus* and *Sennius* that prey on only one species of *Cassia* each, leaving fourteen species of *Cassia* unattacked by them in the study area. Those species of *Megacerus* that prey on only one species of *Ipomoea* ignore eleven other species of *Ipomoea*. If the site is chosen carefully, all fifteen species of *Cassia* and twelve of *Ipomoea* can be found in an area as small as 20 km across.

In most cases, competition between beetles that prey on seeds is very direct. There is generally enough food in one seed for only one beetle larva (e.g. column 7, Appendix 1). Dissection of seeds with many eggs shows that larvae which enter after one is established are usually simply eaten. The exceptions usually involve clutches of sibling larvae in a seed much larger than the beetle larva. As many as thirty-five *Caryedes brasiliensis* may develop simultaneously in one of the huge seeds of *Dioclea megacarpa* and all of these usually come from the cluster of 15- to 25-egged oothecae laid at one site on the pod (Janzen 1971b). Similar cases are reported by Janzen (1971c, 1974b).

When the larva is much larger than a single seed, as is the case with *Amblycerus* spp. preying on seeds of *Guazuma ulmifolia*, *Cassia emarginata*, *C. leptocarpa*, *C. obtusifolia*, *C. uniflora* and *Spondias mombin*, the larva lives outside the seed but inside the fruit and moves from seed to seed, consuming seeds as encountered. These larvae also consume seeds containing larvae of other seed-predators.

## Abundance of beetle seed-predators

Beetles of different species that prey on the same species of plant are usually not equally common in samples of seeds of that species (e.g. Janzen 1971c, 1975c, 1977b). For example, in *Mimosa albida* seed crops, about 88–99% of the beetles to emerge are *Acanthoscelides difficilis*, 0–12% are *A. cordifer*, and 0–1% are *Stator pruininus* (Table 1). The ratios are not always so consistent, however. In *Acacia tenuifolia* seed crops, *Merobruchus terani* can constitute 1–97% of the beetles to emerge from a sample, *Stator vittatithorax* 2–67%, and *S. limbatus* 0–94% (Table 2). On the other hand *Caryedes cavatus* and *C. x-liturus* generally emerge in approximately equal numbers from seed samples of *Bauhinia glabra*, and the beetles *Megacerus cubicus* and *M. maculiventris* generally emerge in approximately equal numbers from large samples of *Ipomoea nil*.

TABLE 1. Bruchid species and number of hymenopteran parasitoids emerging from seed crops of *Mimosa albida* in Santa Rosa National Park (1976–77)

<i>Mimosa albida</i> crop number	<i>Acanthoscelides difficilis</i> (%)	<i>Acanthoscelides cordifer</i> (%)	<i>Stator pruininus</i> (%)	Total* beetles reared	Number of parasitoids
1	96	3	1	115	4
2	96	3	1	468	0
3	97	2	1	412	5
4	99	0	1	177	0
5	99	1	0	505	27
6	98	2	0	410	1
7	88	12	1	203	6
8	99	1	0	812	29
9	99	0	1	201	0
10	99	1	0	354	0
11	99	0	1	251	0

\* Samples containing more than 200 *Acanthoscelides difficilis* individuals were rounded to the nearest 50.

TABLE 2. Bruchid species and number of parasitoids in seed crops of *Acacia tenuifolia* in Santa Rosa National Park (1976–77)

<i>Acacia tenuifolia</i> crop number	<i>Merobruchus terani</i> %	<i>Stator vittatithorax</i> %	<i>Stator limbatus</i> %	Total beetles reared	Number of parasitoids
1	24	17	59	46	0
2	33	67	0	30	2
3	1	5	94	84	0
4	14	50	31	195	6
5	14	45	41	122	0
6	97	2	1	282	0

## Consistency of attack

In more than 90% of the samples from the species with multiple beetle seed-predators, all of the beetle species which attack that seed species in the habitat were present. If only one species attacked the seeds, it was commonplace for it to be reared from all large samples (column 6, Appendix 1). For example, *Amblycerus cistelinus* occurred in all 227 samples of *Guazuma ulmifolia*, *Caryobruchus buscki* in all 148 samples of *Scheelea rostrata*, and *Merobruchus columbinus* in all ninety-five samples of *Pithecellobium saman*. In 124 cases (80%), the beetle was found in the first seed sample collected (column 5, Appendix 1);



in fifteen cases (10%), the association was made in the second or third sample. In only sixteen cases (10%), was the association made in the fourth or later samples. In almost all of these sixteen cases, there are good biological reasons for this tardiness. Some beetles are very rare. For example, there was about one *Ctenocolum salvini* (found in the tenth sample of *Dalbergia retusa*) per 1000 fruits at SRNP and the beetle has not yet been found in the southern part of the study area (where *D. retusa* is a moderately common tree.) Some tardy records may be abnormal. *Gibbobruchus guanacaste* was found only in the sixth sample of *Bauhinia glabra* seeds, although it is very abundant in samples of the sympatric *Bauhinia unguolata*. Some late associations may be artifacts. *Megasennius muricatus* was found late in *Cassia grandis* (fifteenth sample) because it occurs only in the southern part of the study area and this was sampled late in the study. Samples of *Aeschynomene americana* from roadside ditches alongside pastures usually have no bruchids in them, and it was not until samples were obtained from roadsides in forest that *Meibomeus surrubresus* was encountered. Some beetles depend on interactions with other animals for seed predation. *Rhinochenus stigma* is very rare in seed crops of *Hymenaea courbaril* in habitats where agoutis have been exterminated by hunting or forest clearance, because this weevil is dependent on the agouti to open the indehiscent pod if the adult beetle is to escape (Janzen 1975b). In general, the beetles are very efficient at locating the seed crops of individual plants.

#### *Survival of adult beetles*

If a beetle species has a single prey species, then adults, when they emerge from the seeds and fruits, spend the next 9–10 months relatively active at large in the habitat and have been found by trapping of various kinds (Malaise\* traps, sugar baits, sweep samples, light traps). They are especially frequently encountered resting inside rolled leaves and in flowers. No species has remained dormant in seeds or fruits in the samples held in the laboratory, nor has any been found in the field. There may be more than one generation per year if there is more than one prey species or if the prey bears susceptible seeds or fruits for several months. However, every species must deal with 4–10 months with no seeds or fruits. In the laboratory, bruchids lay more eggs and live longer if fed honey and pollen. In nature the free-ranging beetles concentrate in local, moist and shady sites during the dry season and eat pollen and nectar at all times of the year.

#### *Other seed-predators*

Other insects in the study area attack seeds in the same way as do predators. The seeds of *Annona reticulata* (Annonaceae) are preyed on while still in the maturing fruit by the monophagous larvae of the chalcid wasp *Bephratelloides cubensis* (Ashmead). The minute seeds of *Chlorophora tinctoria* (Moraceae) are eaten, while developing, by small fly larvae (Cecidomyiidae). The large bostrychid beetle *Melalgus excelsus* (Leconte) mines in dry hard fruits such as those of *Annona reticulata* and *Cassia grandis*. Unidentified moth larvae feed on the still soft full-sized seeds of *Ateleia herbert-smithii*, *Bauhinia unguolata*, *Caesalpinia eriostachys*, *Canavalia brasiliensis*, *Cedrela odorata*, *Gliricidia sepium*, *Pachyrhizus erosus*, and others. However, the damage done by such species is generally small compared to the pre- and immediately post-dispersal seed-predation by the Coleoptera listed in Appendix 1. At the flower and immature fruit stages, there is heavy predation by

\* A tent trap. Beetles flying into the trap move to the highest point, where there is a collecting bottle.

parrots, squirrels, sucking bugs (Hemiptera), weevils (e.g., three species of *Anthonomus* in the flower buds of *Hymenaea courbaril*) and moth larvae (see, for example, Bawa & Opler (1978)). Once the seeds are dispersed, granivorous birds and rodents and sucking bugs (e.g. *Dysdercus* spp. that prey on *Bombacopsis quinata* and *Sterculia apetala* seeds—Janzen (1972 and unpublished)) are the major seed-predators.

#### Parasitoids

Of the 157 sets of rearings of a given beetle species from a particular seed species, 57% of the beetle species were unattacked by hymenopterous parasitoids (column 10, Appendix 1). This startling result suggests that the interaction of plants with seed-predator beetles is in the large part determined by traits of the plant and its beetles rather than by the third-order interactions so prominent in extra-tropical forests. Of the 110 beetle species listed in Appendix 1, 59% had no species of hymenopterous (or other arthropod) parasitoid reared from them when preying on the seeds of any of their prey species. In most of the remainder, fewer than 5% of the insects emerging from a sample were parasitoids (e.g. Tables 1 and 2). In some cases, parasitoids were found in the sample only when the beetle was attacking one of several of its species of prey seeds. The samples of a few species, however, often generated as many parasitoids as beetles (e.g., *Gibbobruchus guanacaste* in *Bauhinia unguolata*, *Mimosestes* spp. in *Acacia farnesiana* and *Acacia* new sp., *Merobruchus* spp. in *Albizia* spp., *Caryedes quadridens* in *Centrosema plumieri*, *Stator limbatus* in *Pithecellobium oblongum*, *Stator pruininus* and *Acanthoscelides griseolus* in *Sesbania emerus*, and others). As many as 30% of the larvae of the two species of bruchids in *Scheelea rostrata* palm nuts are killed by a milky spore bacterial disease (Janzen 1971a).

In contrast, no parasitoids were found in hundreds of samples of common seed-predators in large samples from common plants: *Merobruchus columbinus* in *Pithecellobium saman*, *Amblycerus cistelinus* in *Guazuma ulmifolia*, *Megacerus leucospilus* in *Ipomoea pes-caprae*, *Mimosestes mimosae* in *Caesalpinia coriaria*, *Pygiopachymerus lineola* in *Cassia grandis* and *Rhinochenus* spp. in *Hymenaea courbaril* (column 3, Appendix 1). In the 1978–79 samples of *Ateleia herbert-smithii*, well over a million *Apion* adults emerged but only thirteen individuals (four species) of hymenopterous parasitoids emerged. In short, trees such as *Pithecellobium saman* or *Guazuma ulmifolia* support tens of thousands of bruchids every year but very few parasites. When there were hymenopterous parasitoids in a seed sample, the number of species usually ranged from one to four and the same species was reared from many species of beetles. Whitehead (1975) and Center & Johnson (1976) reported similar results. There seems to be a sparse and species-poor parasitoid fauna spread thinly over a number of species of coleopterous hosts. Possible causes of this relative freedom from parasitoids have been discussed elsewhere (Janzen 1975a, 1977g; Janzen & Pond 1975).

## DISCUSSION

### *The distribution of predators among prey*

The distribution of predator species among prey species is conspicuously non-random. There is a flora of about 875 unattacked species of plants. Within the 100 attacked species of plants, there are 163 cases of seed-predator attack. An expected distribution of these 163 attacks was determined by assuming that they are placed at random on 975 species of plant. The expected number of species with no attackers, one attacker, two, and so on

up to five attacking species of beetle is 825, 138, 11.5, 0.6, 0.03, 0.001. These numbers differ significantly from those observed: 875, 59, 25, 11, 4, 1 ( $\chi^2 = 117$ , d.f. = 2,  $P \ll 0.001$ ). There are too many unattacked species, too few that are preyed on by only one beetle species, and too many that are preyed on by two to five species. This implies that most species of plant have had exceptionally good defences against bruchid attack over evolutionary time and some have been exceptionally susceptible. These results also imply that when a new successful attack occurs, it is more likely to occur on a previously attacked species than on a previously unattacked species. Two processes may produce such contagion. A seed susceptible to predation by one species of beetle may simply lack effective defences against beetle larvae in general, or it may be that the plant has evolved to satiate seed-predators by producing many poorly-defended seeds (Janzen 1969) which may, in turn, increase susceptibility to other species of beetles.

#### *The causes of specificity*

For no species of beetle seed-predator in the study area do we know why it is so prey-specific—an average of only 1.45 seed species per beetle species. The majority of species in the study area do not have an insect that preys on the seeds while living in them, so their non-use by beetles cannot be due to any direct form of competitive exclusion by some other insect. Non-use may be in part due to competition with the remainder of the herbivores feeding on the plant, mediated through the impact of all these animals on the resource budget of the plant over evolutionary time (Janzen 1973d), but this is unlikely to be the entire story. It seems very probable that the particular complex of traits of the fruits and seeds of unattacked species (annual and longer-term phenology, secondary-compound chemistry, nutrient chemistry, size, morphology, density, habitat occupied, etc.) is sufficient, at present, to protect the plants against the combined abilities of all the existing seed-eating beetles in the area.

Some parts of this hypothesis are plausible. Many of the compounds, at the concentration found naturally in seeds in the study area, are toxic to at least one bruchid species (Janzen 1977f; Janzen, Juster & Bell 1977). Many morphological traits of fruits and seeds appear likely to deter beetle seed-predators (Janzen 1969; Center & Johnson 1974; Janzen 1977f; Mitchell 1977). The timing of fruit production within and between years probably evolved at least in part under pressure from seed-predators (Janzen 1978c).

#### *Chemical interactions*

When an understanding of the basis for the extreme prey-specificity documented in Appendix 1 is sought, the cases with three or more prey species are instructive. On the one hand, *Ctenocolum crotonae* and *C. tuberculatum* each prey on the same three species of *Lonchocarpus* out of the six in the study area. Incomplete analysis of the chemistry of *Lonchocarpus* seeds shows that each of these three contains the same two relatively toxic compounds similar to alkaloids and non-protein amino-acids (L. Fellows & E.A. Bell, personal communication). On the other hand, *Stator limbatus* and *S. pruininus* each prey on seeds in three or four genera. Such a varied diet requires the ability to detoxify or avoid a large variety of secondary compounds. Viewed over their entire range (south-western U.S.A. to northern South America), these two beetles have really remarkable predatory abilities. Johnson & Kingsolver (1976) list twenty-four prey species for *Stator limbatus* and forty-four for *S. pruininus*.

In only one case are some details known (Rosenthal, Dahlman & Janzen 1976, 1978; Rosenthal, Janzen & Dahlman 1977). *Caryedes brasiliensis* is prey-specific to *Dioclea*

*megacarpa*, at least in part because its protein synthesis processes can distinguish between arginine and the potentially toxic non-protein amino-acid, canavanine—a compound that occurs in high concentration in *D. megacarpa* seeds. It also has the ability to degrade canavanine and use the products in protein synthesis; it may even be dependent on canavanine. But why does *Caryedes brasiliensis* not prey on the large canavanine-rich seeds of the sympatric and closely related *Canavalia brasiliensis*, which has no pre-dispersal coleopterous seed-predator in the study area? Some other *Canavalia* species in other parts of Costa Rica are preyed on by other species of *Caryedes*. Furthermore, it is puzzling that the ability to detoxify *Dioclea megacarpa* seeds should preclude the ability to detoxify other seeds. *Stator pruininus*, for example, can prey on the canavanine-rich, minute seeds of *Sesbania emerus* as well as the seeds of five other species (Appendix 1) which do not contain canavanine but are rich in other non-protein amino-acids (E. A. Bell, personal communication). Perhaps it is that the *Stator pruininus* of the taxonomist is two or more sympatric populations, each with different biochemical abilities.

The most puzzling cases are those where there are a number of species of the same genus occupying the same area, and whose seeds are not preyed on by any of the beetles that attack one or more members of the genus. Why are the seeds of *Ipomoea alba* and *I. imbracticola* not preyed on by one of the six species of *Megacerus* that attack eight other species of largely sympatric *Ipomoea* in the study area? Why does *Mimosestes mimosae* heavily attack two species of *Acacia*, *Caesalpinia coriaria* and *Parkinsonia aculeata* and ignore four species of woody *Acacia* and three of *Caesalpinia* in the study area? *Caesalpinia bonduc*, *C. exostemma* and *C. vesicaria* have seeds that are quite large enough for a *Mimosestes mimosae* larva to develop in and yet they are not attacked by any species of Coleoptera.

Leguminosae constitute 65% of the prey records in Appendix 1, though only 17% of the flora is in the Leguminosae. Legume seeds generally contain protease inhibitors, and the two species of bruchids examined by Applebaum (1964) lacked gut proteases. It may be that the non-leguminous species listed in Appendix 1 also rely heavily on protease inhibitors for defence, and are consequently susceptible to attack by bruchids. Alternatively they may simply lack secondary-compound defences, as is suggested by the tough nut in which many are imbedded (e.g. *Hippomane mancinella*, *Scheelea rostrata*, *Spondias mombin*, *S. radlkoferi*).

Convolvulaceae are worth close examination in this context. They have their own genus of distinctive bruchids (*Megacerus*) and the seeds of Convolvulaceae are generally rich in alkaloids. Alkaloids are prominent parts of the defences of some legume seeds too and there are bruchids known to prey on alkaloid-rich legume seeds (e.g. *Specularius* spp. on various African species of *Erythrina* (Bridwell 1938; Kingsolver & Decelle 1979). This suggests that the evolution of the ability to eat seeds of the Convolvulaceae probably happened only once, followed by radiation based on an alkaloid-resistant physiology as is assumed by Teran & Kingsolver (1977).

#### Other causes of specificity

Chemistry is of course not the only trait of a seed that influences which beetle species can prey on it. For example, the larvae of many of the beetles listed in Appendix 1 require a much larger seed for development than is produced by many of the species of unattacked plants in the study area. Fruit traits are also important. For example, all the eight species fed on by *Stator limbatus* in the study area have flat, thin-walled, dry dehiscent fruits except for *Pithecellobium saman* which can be attacked only when the beetle

can gain access through a break in the thick and indehiscent fruit wall. In the other seven species, eggs are laid on the seeds as the fruit dehisces, or on the dry fruit wall directly above the seeds. Even more odd is *Caryedes*, every species of which, in the study area, preys on the seeds of a vine or liana (five genera of Leguminosae).

It may be that time is needed for the seed-predator to spread to its maximum possible range. The common neotropical tree, *Enterolobium cyclocarpum*, has no coleopterous seed-predators in the study area, yet in Panama at least *Stator generalis* preys on the seeds (C. D. Johnson, personal communication). Has this beetle simply not yet arrived in Central America and Mexico? Is the same happening with *Desmodium barclayi* and *D. glabrum*, common fabaceous legume vines with large seed crops in Santa Rosa National Park? Neither plant has a beetle seed-predator, yet *Desmodium* is a well known prey-genus for *Meibomeus* in other parts of Central and North America.

#### *Consequences of specificity*

The potential effects on their prey of the high prey-specificity of these beetle seed-predators have been discussed earlier (Janzen 1969, 1970, 1978c). However, there is no way to query if the very high levels of seed predation (Janzen 1971a, 1975c, 1977b, 1978a; Wilson & Janzen 1972) would have been different had each bruchid had more than one species of prey in the study area. Would *Stator limbatus* attack *Pithecellobium platylobum* or *Acacia tenuifolia* less severely if it did not have seven other sympatric prey species? There are roughly equally plausible theoretical reasons for expecting that change in the number of species on the prey list of any species of beetle seed-predator will raise, lower, or not influence the intensity of seed predation on a given host. What actually happens depends on the details of the natural history of the species in its habitats. We can only work out a series of unique cases, and then determine a frequency distribution of answers.

#### *Other problems*

It is commonplace for a seed-predator to have quite different prey-species in different parts of its range. *Sennius morosus* has been reared from the seeds of *Cassia leptocarpa* in Arizona (Johnson 1977c), yet in the study area it has been reared only from *Cassia obtusifolia* though *C. leptocarpa* is common in the study area and is fed on by five other species of bruchids (Appendix 1), none of which occurs in Arizona.

On a smaller scale, there are five unambiguous cases of a prey species occurring throughout the study area but having two seed-predators whose ranges do not overlap in the study area. *Mimosa pigra* is preyed on exclusively by *Acanthoscelides zebratus* northwards from La Cruz, and exclusively by *A. quadridentatus* to the south of this point. *Pterocarpus rohrii* is attacked only by *Amblycerus pterocarpi* at SRNP and only by *Apion pterocarpi* at COMELCO (*Pterocarpus rohrii* has not been sampled in between). *Ipomoea carnea* is attacked by *Megacerus cubicus* and *M. ramicornis* at SRNP but by *M. leucospilus* at COMELCO (Palo Verde National Park). *Centrosema pubescens* is preyed on by *Caryedes helvinus* in the vicinity of SRNP but by *C. incensus* in the southern part of the study area. *Rhynchosia minima* is preyed on by *Acanthoscelides zeteki* in SRNP while it is preyed on by *A. flavescens* from the Cañas area to the south. It is easy to imagine that this type of distribution is due to a change in climate along the boundary where seed predation by one beetle changes to that by another (for example, the range of *A. zebratus* is more moist than the range of *A. quadridentatus* in the study area). There is such a range of microclimate in any one locality, however, that it seems very unlikely that the habitat required by each beetle would not be found within the range of the other. Equally

unappealing is the hypothesis of direct competitive exclusion of one beetle by the other. Of the pairs mentioned above, only in the case of *Pterocarpus rohrii* is seed predation sufficiently intense that there might be direct competition for seeds.

## CONCLUSION

Thirteen years ago, it seemed interesting to know how prey-specific were the insects that feed on seeds. It still seems so, but it is worth emphasizing that the prey-specificity of herbivorous insects is only one factor affecting the structure of tropical forests (Janzen 1970). The hypothesis, sometimes used, that animals are entirely responsible for the variation in plant species-richness on the earth's surface is much too simple. Even worse, the act of being host- or prey-specific by herbivores has sometimes been taken as the linchpin of this hypothesis. Animals may be a major factor, but they are not necessarily the sole or major force in generating within- or between-habitat variation in plant species-richness. Furthermore, an animal need not be highly specific to have an impact, and high specificity does not guarantee high impact.

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## APPENDIX 1

Prey-specificity of lowland Guanacaste beetle seed-predators that live in fruits and seeds: superscripts refer to footnotes. Key to column headings: (1) Beetle name. (2) Known prey seed species<sup>1</sup>. (3) Minimum number of seed samples<sup>2</sup>. (4) Approximate number of seeds in a representative sample<sup>3</sup>. (5) Sample in which first found. (6) Percent of samples containing this species. (7) Number of beetles that can develop in a seed. (8) Number of species of beetles preying on this species<sup>4</sup>. (9) Number of lowland Guanacaste congeners unattacked by this beetle<sup>5</sup>. (10) Hymenopterous parasitoids present in one or more samples<sup>6</sup>. (11) Relevant references, at the end of footnotes.

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
Bruchidae:										
<i>Acanthoscelides argillaceus</i>	<i>Phaseolus lunatus</i>	31	600	1st	87	1-2	2	5	yes	5
<i>Acanthoscelides brevipes</i>	3 species of <i>Sida</i> <sup>28</sup>	11	500	1st	100	0.25-0.5	1	8 <sup>28</sup>	no	
<i>Acanthoscelides clitellarius</i>	<i>Piptadenia flava</i>	3	200	1st	67	1	4	NA	no	
<i>Acanthoscelides cordifer</i>	<i>Mimosa albida</i>	18	1000	1st	89	1	3	9	yes	
	<i>Mimosa guanacastensis</i>	15	300	1st	100	1	3	9	no	
<i>Acanthoscelides devriesi</i>	<i>Mimosa dormiens</i>	6	1000	1st	100	1	1	10	no	41
<i>Acanthoscelides difficilis</i>	<i>Mimosa albida</i>	18	1000	1st	100	1	3	8	yes	
	<i>Mimosa guanacastensis</i>	15	300	1st	100	1	3	8	no	
	<i>Mimosa pudica</i>	6	500	2nd	50	1	1	8	no	
<i>Acanthoscelides flavescens</i>	<i>Rhynchosia minima</i> <sup>27,39</sup>	8	100	1st <sup>39</sup>	78 <sup>39</sup>	1	1 <sup>27</sup>	2	no	
<i>Acanthoscelides griseolus</i>	<i>Sesbania emerus</i>	26	10 000	1st	100	1	2	NA	yes	12, 21
<i>Acanthoscelides guazumae</i> <sup>32</sup>	<i>Guazuma ulmifolia</i> <sup>33</sup>	227	6000	3rd	7	1	2	NA	no	
<i>Acanthoscelides kingsolveri</i>	<i>Indigofera costaricensis</i>	9	5000	1st	100	1	1	3	yes	18, 19
	<i>Indigofera suffruticosa</i>	21	5000	1st	100	1	1	3	no	18, 19
<i>Acanthoscelides petalopygus</i>	<i>Acacia collinsii</i>	13	300	2nd	15	1	2	6	no	42
<i>Acanthoscelides megacornis</i>	<i>Aeschynomene americana</i>	11	1000	2nd	73	1	3	4	no	
<i>Acanthoscelides mexicanus</i>	<i>Mimosa</i> aff. <i>eurycarpa</i>	13	1000	1st	100	1	1	10	no <sup>29</sup>	
<i>Acanthoscelides obrienorum</i>	<i>Cassia biflora</i> <sup>34</sup>	40 <sup>34</sup>	1000	3rd <sup>34</sup>	30 <sup>34</sup>	1	3	13 <sup>34</sup>	yes	
	<i>Cassia skinneri</i>	8	100	1st	100	1	1	13	yes	
<i>Acanthoscelides pertinax</i>	<i>Aeschynomene americana</i>	11	1000	2nd	73	1	3	4	no	
<i>Acanthoscelides puellus</i>	<i>Calopogonium mucunoides</i>	16	300	1st	100	1	1	1	yes	
<i>Acanthoscelides quadridentatus</i> <sup>30</sup>	<i>Mimosa pigra</i> <sup>30</sup>	31 <sup>30</sup>	500	1st <sup>30</sup>	100 <sup>30</sup>	1	1	10	no	10
<i>Acanthoscelides hectori</i> <sup>26</sup>	<i>Calopogonium caeruleum</i>	4	400	1st	100	1	2	1	no	42
<i>Acanthoscelides triumfettae</i>	<i>Triumfetta lappula</i>	8	500	1st	100	1	1	1	no	
<i>Acanthoscelides zebratus</i> <sup>31</sup>	<i>Mimosa pigra</i> <sup>31</sup>	5 <sup>31</sup>	500	1st <sup>31</sup>	100 <sup>31</sup>	1	1	10	no	10, 41
<i>Acanthoscelides zeteki</i>	<i>Rhynchosia minima</i> <sup>27,40</sup>	3 <sup>40</sup>	100	1st <sup>40</sup>	100 <sup>40</sup>	1	1 <sup>40</sup>	2	no	23
<i>Algarobius bottimeri</i>	<i>Prosopis juliflora</i>	16	2000	1st	100	1	4	NA	yes	
<i>Amblycerus biolleyi</i>	<i>Cordia alliodora</i>	22	1000	1st	100	1	2	8	yes	

<i>Amblycerus obscurus</i>	<i>Cassia leptocarpa</i>	10	1000	1st	100	0.05-0.1	5	14	no	
	<i>Cassia obtusifolia</i>	20	800	1st	100	0.05-0.1	3	14	no	
	<i>Cassia uniflora</i>	8	800	1st	100	0.1-0.2	1	14	no	
<i>Amblycerus championi</i> <sup>23</sup>	<i>Cordia panamensis</i>	7	100	1st	100	1	1	8	no	
<i>Amblycerus cistelinus</i>	<i>Guazuma ulmifolia</i>	227	6000	1st	100	0.02-0.05	2	NA	no <sup>24</sup>	12, 2
<i>Amblycerus epsilon</i>	<i>Cassia emarginata</i>	12	5000	1st	100	0.05-0.1	1	14	yes	42
<i>Amblycerus geminatus</i>	<i>Banisteriopsis muricata</i>	6	200	1st	83	1	1	1	no	
<i>Amblycerus dytiscinus</i>	<i>Cissus rhombifolia</i>	3	30	1st	33	1	1	1	no	
<i>Amblycerus imperfectus</i>	<i>Combretum farinosum</i>	30	200	10th	37 <sup>19</sup>	1	3	NA	no	42
<i>Amblycerus new species</i> <sup>45</sup>	<i>Prosopis juliflora</i>	16	2000	2nd	75	0.25-0.5	4	NA	yes	
<i>Amblycerus multiflocculus</i>	<i>Banisteriopsis cornifolia</i>	1	100	1st	100	1	1	1	no	
	<i>Heteropterys beecheyana</i>	1	200	1st	100	1	1	1	no	
<i>Amblycerus perfectus</i>	<i>Combretum farinosum</i>	30	200	1st	100	1	3	NA	no	
<i>Amblycerus pterocarpae</i> <sup>25</sup>	<i>Pterocarpus rohrii</i> <sup>25</sup>	5 <sup>25</sup>	300	1st <sup>25</sup>	100 <sup>25</sup>	1-2 <sup>25</sup>	1 <sup>25</sup>	NA	no	42
<i>Amblycerus baracoensis</i>	<i>Cordia gerascanthus</i>	11	500	1st	100	1	1	8	no	
<i>Amblycerus spondiae</i>	<i>Hippomane mancinella</i>	13	200	1st	92	1	1	NA	no	
	<i>Spondias mombin</i>	22 <sup>20</sup>	300	1st	100	0.3-0.5	1	0 <sup>22</sup>	no	
	<i>Spondias radlkoferi</i> <sup>21</sup>									
<i>Amblycerus vegai</i>	<i>Cordia alliodora</i>	22	1000	1st	100	1	2	8	yes	42
<i>Caryedes brasiliensis</i>	<i>Dioclea megacarpa</i>	55	80	1st	93	1-35	1	NA	no	7, 28, 30-32
<i>Caryedes cavatus</i>	<i>Bauhinia glabra</i>	6	200	1st	83	1	3	3	no	28
<i>Caryedes helvinus</i>	<i>Centrosema pubescens</i>	10 <sup>43</sup>	300	1st	100 <sup>43</sup>	1	1	2	yes	28
<i>Caryedes incensus</i>	<i>Centrosema pubescens</i>	5 <sup>44</sup>	300	1st	100 <sup>44</sup>	1	1	2	yes	28
<i>Caryedes junco</i>	<i>Galactia striata</i>	25	300	1st	40	1	1	NA	yes	28
<i>Caryedes paradisiensis</i>	<i>Calopogonium caeruleum</i>	4	400	1st	75	1	2	1	yes	28
<i>Caryedes quadridens</i>	<i>Centrosema plumieri</i>	18	80	1st	100	1	1	2	yes	28
<i>Caryedes x-liturus</i>	<i>Bauhinia glabra</i>	6	200	1st	83	1	3	3	no	28
<i>Caryobruchus buscki</i>	<i>Scheelea rostrata</i>	148	100	1st	100 <sup>10</sup>	1	2	NA	no <sup>9</sup>	2, 6, 40
<i>Ctenocolum acapulcensis</i>	<i>Lonchocarpus eriocarinalis</i>	20	100	1st	100	1	2	5	no	27
<i>Ctenocolum biolleyi</i>	<i>Lonchocarpus eriocarinalis</i>	20	100	5th	65	1	2	5	no	27
<i>Ctenocolum crotonae</i>	<i>Lonchocarpus costaricensis</i>	33	200	1st	55	1-2	2	3	no	27
	<i>Lonchocarpus nitidus</i>	21	1000	1st	100	1	2	3	yes	27
	<i>Lonochocarpus parviflorus</i>	17	500	1st	100	1	2	3	yes	27
	<i>Piscidia carthagenensis</i>	9	1000	1st	100	1	2	NA	no	27
<i>Ctenocolum janzeni</i>	<i>Piscidia carthagenensis</i>	9	1000	1st	100	1	2	NA	no	27
<i>Ctenocolum salvini</i>	<i>Dalbergia retusa</i>	14	2000	10th <sup>13</sup>	14 <sup>13</sup>	1	1	NA	no	27
<i>Ctenocolum tuberculatum</i>	<i>Lonchocarpus costaricensis</i>	33	200	1st	94	1-2	2	3	no	27
	<i>Lonchocarpus nitidus</i>	21	1000	1st	100	1	2	3	yes	27
	<i>Lonchocarpus parviflorus</i>	17	500	1st	53	1	2	3	yes	27

(continued)

## Appendix 1—continued

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
<i>Gibbobruchus cristicollis</i>	<i>Bauhinia pauletia</i>	46	400	1st	83 <sup>14</sup>	1	2	1	yes	16, 17, 37
<i>Gibbobruchus guanacaste</i>	<i>Bauhinia glabra</i>	6	200	6th	17	1	3	1	no	37
	<i>Bauhinia pauletia</i>	46	400	1st	24	1-2	2	1	yes	16, 17, 37
	<i>Bauhinia unguolata</i>	43	200	1st	100	1	1	1	yes	37
<i>Megacerus bifloccosus</i>	<i>Merremia umbellata</i>	12	800	1st	83	1	2	2	yes	34
<i>Megacerus cubicus</i>	<i>Ipomoea carnea</i> <sup>42</sup>	6 <sup>42</sup>	400	1st	100 <sup>42</sup>	1	2 <sup>42</sup>	9	yes	34
	<i>Ipomoea meyeri</i>	8	400	1st	100	1	1	9	no	34
	<i>Ipomoea nil</i>	11	200	1st	100	1	2	9	no	34
<i>Megacerus flabelliger</i>	<i>Ipomoea hederifolia</i>	8	200	2nd	88	1	1	10	yes	34
	<i>Merremia umbellata</i>	12	800	1st	100	1	2	2	yes	34
<i>Megacerus leucospilus</i> <sup>11</sup>	<i>Ipomoea carnea</i> <sup>41</sup>	20	400	1st <sup>41</sup>	88 <sup>41</sup>	1	1 <sup>41</sup>	9	no	34
	<i>Ipomoea fistulosa</i>	10	400	1st	100	1	1	9	no	34
	<i>Ipomoea pes-caprae</i>	26	1200	1st	100	1	1	9 <sup>12</sup>	no	34, 39
<i>Megacerus lherminieri</i>	<i>Jacquemontia tamnifolia</i>	4	300	1st	100	1	1	3	no	34
<i>Megacerus maculiventris</i>	<i>Ipomoea nil</i>	11	200	2nd	82	1	2	11	no	34
<i>Megacerus porosus</i>	<i>Merremia aegyptica</i>	13	400	1st	100	1	1	2	no	34
<i>Megacerus ricaensis</i>	<i>Ipomoea trifida</i>	15	200	12th	20	1	1	11	yes	34
<i>Megacerus ramicornis</i>	<i>Ipomoea carnea</i> <sup>42</sup>	6 <sup>42</sup>	400	1st	83 <sup>42</sup>	1	2 <sup>42</sup>	11	yes	34
<i>Megasennius muricatus</i>	<i>Cassia grandis</i>	52	800	15th	62 <sup>15</sup>	1	3	14	no	29
<i>Meibomeus surrubresus</i>	<i>Aeschynomene americana</i>	11	1000	11th	9	1	3	4	no	43
<i>Merobruchus santarosae</i>	<i>Piptadenia flava</i>	3	200	1st	100	1	4	NA	yes	42
<i>Merobruchus boucheri</i>	<i>Pithecellobium mangense</i>	8	2000	1st	100	1	1	5	no	42
<i>Merobruchus columbinus</i>	<i>Pithecellobium saman</i>	95	300	1st	100	1	2	5	no	14
<i>Merobruchus hastatus</i>	<i>Piptadenia flava</i>	3	200	1st	100	1	4	NA	yes	42
<i>Merobruchus insolitus</i>	<i>Albizzia adinocephala</i>	14	1000	3rd	7	1	4	2	yes	
	<i>Lysiloma seemannii</i>	12	1000	1st	100	1	2	1	yes	
<i>Merobruchus paquetae</i>	<i>Albizzia adinocephala</i>	14	1000	1st	100	1	4	1	yes	42
	<i>Albizzia caribaea</i>	11	500	1st	100	1	3	1	yes	
<i>Merobruchus sonorensis</i>	<i>Albizzia adinocephala</i>	14	1000	1st	100	1	4	1	yes	42
	<i>Albizzia caribaea</i>	11	500	1st	100	1	3	1	yes	
	<i>Lysiloma seemannii</i>	12	1000	1st	100	1	2	1	yes	
<i>Merobruchus terani</i>	<i>Acacia tenuifolia</i>	12	500	1st	100	1	3	6	yes	42
<i>Mimosestes amicus</i>	<i>Parkinsonia aculeata</i>	15	500	1st	87	1	2	NA	no	
	<i>Prosopis juliflora</i>	16	2000	1st	100	1	4	NA	yes	
<i>Mimosestes mimosae</i>	<i>Acacia farnesiana</i>	52	500	1st	100	1	2	5	yes	10 <sup>18</sup>
	<i>Acacia new species</i>	52	500	1st	100	1	2	5	yes	10 <sup>18</sup>
	<i>Caesalpinia coriaria</i>	16	1000	1st	100	1	2	4	yes	
	<i>Parkinsonia aculeata</i>	15	500	1st	100	1	2	NA	no	

<i>Mimosestes nubigens</i>	<i>Acacia farnesiana</i>	52	500	1st	100	1	2	5	yes	10 <sup>18</sup>
	<i>Acacia new species</i>	52	500	1st	100	1	2	5	yes	10 <sup>18</sup>
<i>Mimosestes viduatus</i>	<i>Acacia collinsii</i>	13	300	1st	100	1	2	5	no	
	<i>Acacia cornigera</i>	8	200	1st	100	1	1	5	no	
<i>Pachymerus new species</i> <sup>7</sup>	<i>Scheelea rostrata</i>	148	100	1st	100 <sup>8,10</sup>	1	2	NA	no <sup>9</sup>	2, 6, 40
<i>Pygiopachymerus lineola</i>	<i>Cassia grandis</i>	52	800	1st	100	1-4	3	14	no	8, 15, 24
<i>Sennius auricomus</i>	<i>Cassia biflora</i>	40	1000	1st	100	1	3	13	yes	22
	<i>Cassia leptocarpa</i>	10	1000	10th	10	1	5	13	no	38
<i>Sennius biflorae</i>	<i>Cassia biflora</i>	40	1000	1st	100	1	3	13	yes	38
	<i>Cassia leptocarpa</i>	10	1000	1st	100	1	5	13	no	22
<i>Sennius breveapicalis</i>	<i>Cassia papillosa</i>	9	150	1st	100	1	1	14	no	22
<i>Sennius ensiculus</i>	<i>Cassia 10969</i>	1	400	1st	100	1	1	14	yes	
<i>Sennius instabilis</i>	<i>Cassia obtusifolia</i>	20	800	5th	10	1	3	14	no	22
<i>Sennius lebasi</i>	<i>Cassia leptocarpa</i>	10	1000	1st	100	1	5	14	no	22
<i>Sennius morosus</i>	<i>Cassia obtusifolia</i>	20	800	5th	10	1	3	14	no	22
<i>Stator championi</i>	<i>Bixa orellana</i>	8	500	1st	100	1	1	NA	no	1 <sup>17,25</sup>
<i>Stator limbatus</i>	<i>Acacia retusa</i>	18	500	16th	11	1	2	5	yes	44
	<i>Acacia tenuifolia</i>	19	500	1st	89	1	3	5	yes	
	<i>Albizzia adinocephala</i>	12	500	1st	100	1	3	1	yes	
	<i>Albizzia caribaea</i>	11	1000	1st	100	1	4	1	yes	
	<i>Piptadenia flava</i> (10356)	3	200	3rd	33	1	4	NA	yes	
	<i>Pithecellobium oblongum</i>	12	400	1st	100	1-5	1	3	yes	
	<i>Pithecellobium platyloba</i>	20	100	1st	100	1-9	1	3	no	
	<i>Pithecellobium saman</i>	95	300	1st	27	1-5	2	3	no	
<i>Stator pruininus</i>	<i>Desmanthus virgatus</i>	4	300	4th	25	1	1	NA	no	
	<i>Mimosa albida</i>	18	1000	3rd	78	1	3	7	yes	
	<i>Mimosa guanacastensis</i>	15	100	3rd	33	1	3	7	yes	
	<i>Mimosa pusilla</i>	8	2000	1st	100	1	3	7	yes	
	<i>Mimosa quadrivalis</i>	12	500	1st	100	1	1	7	no	
	<i>Sesbania emerus</i>	17	10 000	1st	100	1	2	NA	yes	44
<i>Stator sordidus</i>	<i>Combretum farinosum</i>	30	200	22nd	3	1	3	NA	no	44
<i>Stator vittatithorax</i>	<i>Acacia retusa</i>	18	500	1st	100	1	2	5	yes	44
	<i>Acacia tenuifolia</i>	19	500	1st	82	1	3	5	yes	
<i>Zabrotes chavesi</i>	<i>Cassia leptocarpa</i>	10	1000	8th	10	1	5	14	no	42
<i>Zabrotes propinquus</i>	<i>Mimosa pusilla</i>	8	2000	6th	13	1	3	10	yes	
<i>Zabrotes interstitialis</i>	<i>Cassia grandis</i>	52	800	1st	29 <sup>16</sup>	1-8	3	14	no	8, 15
<i>Zabrotes subfasciatus</i>	<i>Phaseolus lunatus</i>	31	600	2nd	40	1-5	2	5	yes	5
Cerambycidae:										
<i>Leptostylus gibbulosus</i>	<i>Sapindus saponaria</i>	9	100	1st	100	1	1	N/A	no	

(continued)

## Appendix 1—continued

(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)
<i>Leptostylus spermatovoratis</i>	<i>Diospyros nicaraguensis</i>	12	50	1st	100	3-6	1	NA	no	3
<i>Leptostylus spermophagus</i>	<i>Manilkara zapota</i>	5	100	1st	100	2-5	2	NA	no	
Curculionidae:										
<i>Achia adusta</i>	<i>Serjania schiedeana</i>	2	200	2nd	50	1	1	3 <sup>38</sup>	no	
<i>Apion glyphicum</i>	<i>Diphysa robinioides</i>	11	200	1st	100	1	1	NA	no	
<i>Apion pterocarpi</i> <sup>35</sup>	<i>Pterocarpus rohrii</i> <sup>35</sup>	9 <sup>35</sup>	300	1st <sup>35</sup>	100 <sup>35</sup>	1 <sup>35</sup>	1	NA	no	36
<i>Apion samson</i>	<i>Andira inermis</i>	250	100	1st	100 <sup>36</sup>	1	4	NA	no	13
<i>Cleogonus armatus</i>	<i>Andira inermis</i>	250	100	2nd	10	1-3	4	NA	yes	13, 33
<i>Cleogonus fratellus</i>	<i>Andira inermis</i>	250	100	1st	50	1-3	4	NA	yes	13, 33
<i>Cleogonus rubetra</i>	<i>Andira inermis</i>	250	100	1st	100	1-3	4	NA	yes	13, 33
<i>Conotrachelus brevirostris</i>	<i>Casearia corymbosa</i>	22	100	1st	50	1	1	6 <sup>37</sup>	no	
<i>Phymatophosus scapularis</i>	<i>Cayaponia attenuata</i>	9	100	1st	100	1	1	0	no	4
	<i>Cayaponia racemosa</i>	11	100	1st	100	2-5	1	0	no	4
<i>Rhinochenus stigma</i>	<i>Hymenaea courbaril</i>	550	400	16th	64	0.2-1	2	NA	no	9, 11, 35
<i>Rhinochenus transversalis</i>	<i>Hymenaea courbaril</i>	550	400	1st	100	1-10	2	NA	no	9, 11, 35
<i>Zygopine</i> , new sp.	<i>Manilkara zapota</i>	5	100	1st	100	1-3	2	NA	no	

<sup>1</sup> Applies only to the lowlands of Puntarenas Province north of Puntarenas and non-peninsular Guanacaste Province, Costa Rica.

<sup>2</sup> A 'sample' was a bag of fruits or seeds collected from a single plant or a cluster of plants of the same species, and ranged from 0.5 to 10 litre in volume. All values are minimum values.

<sup>3</sup> There may be several seeds in a nut or fruit and all seeds in a nut or fruit may be attacked by one beetle larva; this figure multiplied by the number of samples gives a minimum number of seeds from which beetles were reared.

<sup>4</sup> Only species listed in this Appendix are included in this value; moth larvae, sucking bugs, seed chalcids, etc. are excluded. The number of species is the maximum number which can be found in one sample.

<sup>5</sup> Only those species occurring within 10 km of the plant in question are counted; NA = not applicable, as the genus is monospecific in the study area. Only indigenous species are counted.

<sup>6</sup> Only parasitoids that could have been seed chalcids (unlikely) or beetle parasitoids are included. The samples often contained parasitoids of fruit-mining Lepidoptera larvae.

<sup>7</sup> Incorrectly called *Pachymerus cardo* (Fahraeus) in Janzen (1971a).

<sup>8</sup> About 50% in southern Guanacaste as opposed to 100% in northern Puntarenas.

<sup>9</sup> There is a milky-spore-like bacterial disease that kills about 30-40% of the bruchid larvae in the seed about the time of pupation.

<sup>10</sup> Very isolated plants in large pastures often have seed crops totally unattacked by bruchids (Janzen 1971a).

<sup>11</sup> Misidentified as *Megacerus alternatus* in Keeler (1975).

<sup>12</sup> Means that there are nine species of *Ipomoea* in the study area that are not attacked by *Megacerus leucospilus* but occur within 10 km of a plant species that is attacked by *M. leucospilus*.

<sup>13</sup> This beetle was not present in the eleven samples collected south of SRNP and perhaps does not occur in the southern half of the study area.

<sup>14</sup> The beetle-free samples were in plants isolated in open pastures (Janzen 1978a).

<sup>15</sup> This beetle species attacks *Cassia grandis* only in the southern part of the study area.

<sup>16</sup> This beetle species is in all the samples from which *Pygiopachymerus lineola* has emerged but absent from samples of intact fruits.

- <sup>17</sup> In earlier literature incorrectly called *Stator bixae* (Drapiez) (Kingsolver 1976).
- <sup>18</sup> In earlier literature incorrectly called by the junior synonym *Mimosestes sallaei* (Sharp). Also, the predation intensity results reported in Janzen (1975a) were accidentally based on a mixture of samples of *Acacia farnesiana* and a new species of *Acacia*.
- <sup>19</sup> This beetle species attacks this prey only in the northern part of the study area (all records from SRNP).
- <sup>20</sup> This is a mixture of *Spondias mombin* and *Spondias radlkoferi* samples.
- <sup>21</sup> Results are pooled with those of *Spondias mombin*.
- <sup>22</sup> *Spondias purpurea*, which is not attacked in 'nature', is probably introduced as it occurs only in areas of human habitation or use.
- <sup>23</sup> Eggs are laid on the green fruits of *Cordia dentata* but adults never emerge.
- <sup>24</sup> One large yellow chalcid was reared from one fruit (SRNP).
- <sup>25</sup> These statements apply to *Pterocarpus rohrii* only in SRNP; in the southern part of the study area it is preyed on only by a weevil, *Apion pterocarpi*.
- <sup>26</sup> There is one doubtful record, which is probably a plant misidentification, of *A. hectori* from *Rhynchosia minima* in northern Puntarenas Province.
- <sup>27</sup> Take note of footnote 26.
- <sup>28</sup> Species of *Sida* are difficult to identify, so the genus alone is recorded. This beetle was reared from at least 3 taxa of *Sida* in the study area.
- <sup>29</sup> Two parasitic Hymenoptera occurred in two samples containing a total of 504 bruchids.
- <sup>30</sup> Applies only to samples south of La Cruz.
- <sup>31</sup> Applies only to samples north of La Cruz.
- <sup>32</sup> Incorrectly called *Acanthoscelides 'guazumicola'* in Janzen (1975c).
- <sup>33</sup> Called by the junior synonym, *Guazuma tomentosa*, in Johnson & Kingsolver (1971).
- <sup>34</sup> Found only in samples (12) from SRNP.
- <sup>35</sup> These statements apply only to the COMELCO ranch populations of *P. rohrii*.
- <sup>36</sup> Not collected in all samples, but found in fruit under all trees of *A. inermis* if searched for carefully.
- <sup>37</sup> The fruit crops of the other species of *Casearia* are poorly collected so this number may be misleading.
- <sup>38</sup> The fruit crops of the other species of *Serjania* are poorly collected so this number may be misleading.
- <sup>39</sup> Applies only to samples of *Rhynchosia minima* from the area of Finca La Pacifica and to the south.
- <sup>40</sup> Applies only to samples of *Rhynchosia minima* from SRNP.
- <sup>41</sup> Applies only to samples from COMELCO ranch.
- <sup>42</sup> Applies only to samples from SRNP.
- <sup>43</sup> Applies only to samples from the northern part of the study area.
- <sup>44</sup> Applies only to samples from the southern part of the study area.
- <sup>45</sup> This beetle may be *Amblycerus epsilon*.

Key to references in column 11 of Appendix 1; 1, Bentley 1977; 2, Bradford & Smith 1977; 3, Chemsak 1972; 4, Clark 1977; 5, Clegg, Conn & Janzen 1979; 6, Janzen 1971a; 7, Janzen 1971b; 8, Janzen 1971c; 9, Janzen 1974b; 10, Janzen 1975a; 11, Janzen 1975b; 12, Janzen 1975c; 13, Janzen *et al* 1976; 14, Janzen 1977b; 15, Janzen 1977c; 16, Janzen 1977d; 17, Janzen 1978a; 18, Johnson 1973; 19, Johnson 1974; 20, Johnson 1977a; 21, Johnson & Kingsolver 1971; 22, Johnson & Kingsolver 1973; 23, Kingsolver 1969; 24, Kingsolver 1970a; 25, Kingsolver 1970b; 26, Kingsolver & Johnson 1978; 27, Kingsolver & Whitehead 1974a; 28, Kingsolver & Whitehead 1974b; 29, Whitehead & Kingsolver 1975b; 30, Rosenthal, Dahlman & Janzen 1976; 31, Rosenthal, Janzen & Dahlman 1977; 32, Rosenthal, Dahlman & Janzen 1978; 33, Saffer 1977; 34, Teran & Kingsolver 1977; 35, Whitehead 1976; 36, Whitehead 1977; 37, Whitehead & Kingsolver 1975a; 38, Whitehead & Kingsolver 1976; 39, Wilson 1977; 40, Wilson & Janzen 1972; 41, Kingsolver 1980a; 42, Kingsolver 1980b; 43, Kingsolver & Whitehead 1976; 44, Johnson & Kingsolver 1976; 45, Kingsolver 1970c.

## APPENDIX 2

Suspected contaminants or prey transfers in nine of 3700 seed or fruit samples; the number preceding a beetle name is the number of beetles emerging from the sample

Prey species	Usual beetle predator	Suspect beetle	Usual prey of suspect beetle
<i>Cassia leptocarpa</i>	106 <i>Amblycerus obscurus</i>	3 <i>Acanthoscelides brevipes</i>	<i>Sida</i> spp.
	141 <i>Sennius auricomus</i>	1 <i>Acanthoscelides megacornis</i>	<i>Aeschynomene americana</i>
	211 <i>Sennius lebasii</i>	1 <i>Acanthoscelides argillaceus</i>	<i>Phaseolus lunatus</i>
<i>Galactia striata</i>	15 <i>Caryedes juno</i>	1 <i>Acanthoscelides difficilis</i>	<i>Mimosa albida</i> , etc.
<i>Merremia umbellata</i>	23 <i>Megacerus flabelliger</i>	1 <i>Sennius lebasii</i>	<i>Cassia leptocarpa</i>
<i>Mimosa pudica</i>	123 <i>Acanthoscelides difficilis</i>	1 <i>Acanthoscelides cordifer</i>	<i>Mimosa albida</i> , etc.
		3 <i>Acanthoscelides megacornis</i>	<i>Aeschynomene americana</i>
<i>Mimosa quadrivalis</i>	207 <i>Stator pruininus</i>	1 <i>Acanthoscelides brevipes</i>	<i>Sida</i> spp.
<i>Pithecellobium mangense</i>	232 <i>Merobruchus boucheri</i>	2 <i>Merobruchus insolitus</i>	<i>Lysiloma</i> and <i>Albizzia</i>
<i>Pithecellobium platyloba</i>	44 <i>Stator limbatus</i>	1 <i>Algarobius tlacolulae</i>	<i>Prosopis juliflora</i>