

Reprinted from

Biology in Pest and Disease Control

The 13th Symposium of
The British Ecological Society
Oxford, 4-7 January 1972

edited by D. Price Jones and M. E. Solomon

Blackwell Scientific Publications
Oxford London Edinburgh Melbourne
1974

The role of the seed predator guild in a tropical deciduous forest, with some reflections on tropical biological control

DANIEL H. JANZEN *Department of Biology,
University of Chicago, now at Department of Zoology, University
of Michigan, Ann Arbor, Michigan 48104, U.S.A.*

General theory

What effect does the array of animals that kill seeds (and seedlings), henceforth termed the seed predator guild, have on the community structure of the plants in a forest? In north temperate forests, one of the major impacts of the seed predator guild appears to be in the generation of mast year cycles in seed production; this occurs through the mechanism of natural selection against those individual trees that are not synchronized in their fruiting with the majority of their conspecifics or even other unrelated members of the community (Janzen 1971a). I have also argued that it is the generation of mast year behaviour on a population and community-wide basis that prevents the seed predator guild from lowering the density of the dominant tree species to a level where other tree species may invade and thereby increase the richness and diversity of tree species in the forest (Janzen 1970a, 1971a). These arguments, as well as those discussed in the remainder of this presentation, can be applied to foliage-eating animals as well, but will not be discussed further here in that context.

Let us now move to the other end of the gradient of climatic harshness and unpredictability, the lowland tropical evergreen and deciduous forest. Here, we enter habitats where the seed predator guild can be maximally effective at preventing population recruitment by any particular species of forest tree. The result should be that no one forest tree species may competitively displace a wide array of others. This postulation assumes that, given the absence of plant-eating animals or given immunity to them, some small subset of the trees in any complex tropical habitat will be able to multiply to where they competitively displace the others that would also grow there (Janzen 1970a).

In short, I am postulating that the population size of a tree species in a mixed forest is regulated by 'density-dependent' processes just as are animal populations. Further, I am assuming that the phytophagous animal populations in these forests are resource-limited during significant portions of their contemporary (and evolutionary) histories. Finally, I assume that the more favourable are the conditions for the seed predator guild in respect to any particular tree population, the further will that tree's population density (= proximity) have to be depressed by the seed predators before the individual seed crops are so far apart in time and space that the animals can no longer find juvenile plants at a rate that prevents an increase in the population of the tree. The obvious density-dependent mechanism need not be discussed further here. We may, however, recognize that in the case of both seed- and foliage-feeders, a major method of escape by the plants in time and space is through chemically generated inedibility (e.g. Janzen 1971b). We are then confronted with the question of why cannot the animals, and particularly the insects, 'out-run' the plant in the biochemical coevolution game, since they have so many generations during the lifetime of the tree? A formal generalized answer is still in the formulation stage (Janzen & Wolff, unpublished manuscript) but, in short, it appears that it is probably the fate of the average tree population in the lowland tropics to lose the biochemical evolutionary game in a moderately short time to the animals on a local habitat basis. This should result in a high rate of local tree species extinction (and immigration) for any particular habitat over evolutionary time (a rate which is much higher than that to be expected in temperate zone habitats of equivalent geographic size). This higher extinction and immigration rate should also be associated with a higher rate of host-switching in evolutionary time for the more host-specific insects. Incidentally, it must be remembered that all such statements are to be viewed as stochastic in nature, and thus single examples that seem contradictory may simply represent the tails of frequency distributions.

The general postulations set forth in the previous three paragraphs have been generated from a very broad miscellany of data gleaned from the literature, and from my own field work and that of my colleagues in the Central American tropics. Until very recently, almost all the relevant data were gathered for reasons other than the direct examination of these ideas and are not definitive for any given forest or set of ecological conditions. The postulations are put forth for the express purpose of encouraging other workers to gather data on seed and seedling predation, and on foliage parasitization.

In considering these general questions, I have found it always useful to start with a model of the reproduction by a single tree in a single population, and focus my ecological attention primarily at that level. In doing this, I

have found a useful working model (Janzen 1970a). In most generalized terms, this model explores the idea that, on the average, an adult tree in a lowland tropical forest should be most likely to produce another adult at some intermediate distance from its crown. This follows from two observations. Reproduction close to the parent tree is very unlikely, owing to the attacks of incoming and reproducing predators on the seeds and seedlings concentrated below the parent. Reproduction is unlikely far from the parent owing to the low immigration rate of seeds. These two processes should generate an adult spacing pattern far from the contagion expected if only the seed shadow is considered. Now these considerations are of course only relevant if there is any reproduction at all. This proviso is added for the following reason. For any host-specific set of seed predators, a primary source of the seed predators at a specific crop are conspecific crops nearby (in time as well as space); there is a system of mutual infection by all the trees in the area that the insect regards as one 'species' of host. This means that, on the average, the closer a tree is to other conspecifics (with distances measured in ecological rather than metric units), the less likely it is to produce even one new adult. This type of reproductive heterogeneity may also mean that most of the adult trees of a given species may be effectively sterile (despite heavy seed production).

At this point in our brief résumé we could turn in either of two major directions. We could examine the theoretical outcomes, with particular population structures and with aggregate community structures, of modifying the behaviour or abilities of the dispersal agents, the seed predators, and/or the adult trees' reproductive behaviour. Except for a few cases, such as mangroves and some species of Dipterocarpaceae that can persist as pure stands in tropical forests, at present this would be a rather sterile exercise owing to the lack of hard data on the necessary parameters. We have just begun to build a data pool on what the seed shadow of an individual tropical tree looks like. We have almost no information on how tropical seed predators respond to an individual tree's seed crop, nor what is the effect of inter-tree spacing in time and space on tropical herbivores. Finally, we have almost no information on how individual tropical trees modulate their seed production. Some starts in these directions may be found in the following embryonic studies: Janzen (1969, 1971b, 1971c, 1971d, 1972a, 1972b), Wilson & Janzen (1972).

It is probably more profitable at this point to examine some of the more conspicuous assumptions underlying the general model. Data are now beginning to accumulate from a study of deciduous tropical forests in Costa Rica. I may add that, throughout the following discussions, it is evident that an understanding of the systems being described is relevant to the theory of applied ecology (= biological control of insect and weed pests), though

not necessarily to its practice, in tropical countries; I shall, however, save discussion of this area until last.

Host specificity of seed predators

A major background assumption of this study is that the degree and kind of host specificity will influence the predator-prey interaction. Let me immediately add that it is often not clear how it will do so. I have found the seed predator guild of a deciduous forest in Guanacaste Province (Pacific coast lowlands of Costa Rica) to be subdivisible into several major groups on the basis of their type of host specificity. The most host-specific are the beetles (Bruchidae and Curculionidae) whose larvae eat the contents of seeds, usually while the seeds are still within the fruit. They may kill as much as 50 to 99% of a seed crop before it has been dispersed. To date, each of 66 of these species of seed predators (59 bruchids and 7 weevils) has been reared from only one species of host plant (in over 1000 samples of seed crops). Only five species (all bruchids) occur on two hosts (a *Mimosastes* on two *Acacia*, one *Amblycerus* on two *Cassia* and another on two *Cordia*, a *Caryedes* on two *Bauhinia*, and an undescribed bruchid genus on two *Lonchocarpus*) and none on three. These observations should be viewed in the context of a habitat containing about 300 species of woody plants, over half of which have been surveyed in the study. It appears that seed chemistry and fruit behaviour-morphology (e.g. Janzen 1969, 1971a) are the primary traits preventing broader host selection and preferences by the bruchids; it is also tempting to postulate that past millennia of plant-bruchid coevolution have resulted in rather strong character displacement among those traits that are important in defence against these insects. The plant appears to have played the evolutionary game through predator satiation of its host-specific seed predators and chemical-morphological exclusion of its potential seed predators.

There is also an array of insects that feed on fruits, immature seeds, damaged mature seeds, and even mature seeds on occasion. The amount of damage they do is unpredictable and may involve such complex things as destroying the attractiveness of a fruit to a dispersal agent, thereby causing its seeds to be found still on the tree by a seed predator at some later date. Such insects are often highly variable in their host specificity, and will not be considered further here. I should, however, point out that they may be of great importance agriculturally while having little impact on the biology of the plant.

Vertebrates may be divided into at least two groups on the basis of their host specificity. I must add early in this discussion that an individual animal may be classed in either of these two groups at different times, depending on

such things as time of year, reproductive condition of the animal, and site of foraging in the habitat. The first group is made up of those vertebrates that subsist on the seeds of those tropical plants that escape through predator satiation. As in temperate forests, such trees generally produce highly edible (and often wind-dispersed) seeds during a very short period (and sometimes at long intervals, e.g. Dipterocarpaceae). Many vertebrates appear to subsist in great part on such seeds during those times of year when they are produced. Here, the vertebrate may be described as a 'polyphagous' or 'generalist' species, if we measure host specificity by the number of Latin binomials on the host list. I should point out, however, that this is quite different from the generalist that is capable of eating a wide variety of toxic plants. The epitome of escape through predator satiation is probably represented by grasses and palms, neither of which appear to have seeds toxic to seed-eating vertebrates.

On the other hand, there is another kind of polyphagy that appears to be practised by phytophagous vertebrates in tropical vegetation. A large number of tropical seeds contain high concentrations of alkaloids, uncommon amino acids and other poisonous compounds, probably as a primary result of co-evolution with insects. For example, the large seeds of the vine genus *Mucuna* contain 4–8% L-dopa and are not attacked by any insects (cf. Bell & Janzen 1971). Yet such seeds may be eaten in small amounts by small tropical rodents. For example, the seeds of the large forest vine *Dioclea megacarpa* contain 5–10% canavine (a potent arginine competitor in protein synthesis) yet are eaten by squirrels (*Sciurus variegatoides*) in quantities far below their stomach capacity. The result is that during the lifetime of a seed crop, the vine generally loses less than 10% of its seeds to this animal (Janzen 1971b). It appears that small rodents such as this eat only small amounts of a wide variety of toxic seeds during any one period, and thereby do not get enough of any one to overcome their internal detoxication system for that class of compounds (irrespective of whether detoxication is done by the gut microflora or their own biochemical system). This behaviour is probably functionally identical to the habit that ruminants have of browsing small amounts of foliage from each one of a wide variety of dicotyledonous plants, each of which is likely to contain a toxic dose of phenols, alkaloids, cyanogenic glucosides, etc. if eaten in large quantity.

The polyphagous phytophagous rodent that subsists on toxic seeds during all or part of its life cycle is clearly quite a different beast, from the plant's viewpoint, from the polyphagous rodent or other vertebrate that subsists primarily on seeds produced by predator satiators. The former rodent can never move into a local area and eliminate a medium-sized seed crop of toxic seeds, nor can it build up a large population on a locally abundant tree species (as could a host-specific insect). Yet such a rodent exerts a

constant selective pressure against trees that find themselves evolving in the direction of producing a very small number of very large seeds. To stay in the game, such a tree would have to have ever-increasingly toxic seeds. Finally, such rodents (or even larger animals such as deer and peccaries) clearly have less potential as density-dependent population regulators of the trees than do insects or those rodents subsisting primarily on the seeds from trees on the 'predator satiation' adaptive peak.

I might add at this point that most immature fruits appear to be protected by their chemistry alone, and both the rodents and birds (especially parrots) tend to take immature tropical tree seeds in regular but small amounts. Again, this suggests a system where satiation is achieved not through filling the stomach of the predator but through nearly overloading its detoxication abilities.

Parasitization of seed predators

A second major area of background assumptions is associated with the assumption that the seed predators are for the most part resource-limited on both an evolutionary and a contemporary time scale. For the insects, this is suggested by several indirect lines of evidence from the deciduous forest study cited earlier. For the vertebrates, no direct leads have been obtained, but much anecdotal and circumstantial evidence has convinced me that they are likewise resource-limited.

One of the most conspicuous aspects of rearing bruchids and weevils from tropical seeds crops is that many appear to have no parasites. Of the 71 beetle species alluded to earlier, I have reared parasites from only 20. Further, the parasitization is at a level of 1-5% of the emerging adult beetle population, strongly suggesting that the parasites are just 'riding' their host population and having little density-dependent impact on them. A second conspicuous trait of the parasites is that they appear to be highly polyphagous in respect to bruchid species (and probably in respect to other insects as well); one is left with the distinct impression that, to survive in a community where most of the prey species are widely scattered in space and time, the parasite must be polyphagous. It is this observation that suggests why many of the bruchids lack parasites. The parasite is probably not capable of simultaneously possessing the wide array of host-finding behaviours and morphologies that are needed to attack a high number of bruchid species (each with a low density). A high number would be necessary in order to accumulate enough prey individuals to sustain a parasite population. The process is probably the same as that underlying the fact that only a

small fraction of entomophagous parasites have hyperparasites in temperate zones where prey are comparatively abundant.

However, I do not intend to suggest that seed predators are unavailable to general predators. Most of the mortality in the bruchid and weevil population appears to occur when the adults are searching for hosts (and through intraspecific competition in the fruit). However, this predation is probably not density-dependent in action, as no one bruchid species constitutes a large enough fraction of the daily diet of any of the predators (birds, spiders, lizards) to generate any kind of density-dependent response from them if there is a local increase in bruchid or weevil numbers. This means that the insect population density should be most strongly related to the ecological distances in time and space between host plants (as measured in the numbers of beetles that actually pass between hosts, rather than in metric distances between hosts). These distances should in turn be long-term functions of how effective the insects are at killing seeds at any given host plant proximity in time and space.

Related to these queries is the observation that the bruchids are far more evenly distributed among their host plants than would be expected by a randomly operating process. Of the 59 host plants for the 64 bruchids referred to earlier, 48 have only one bruchid using them as a resource base, 9 have two bruchids attacking them, and 2 have three bruchids. This suggests strong competitive displacement among the bruchids in the coevolution of the system. This coevolution may operate on the level of direct interactions between two well-established species, and on the level of an occupant species preventing a second species from shifting onto the host 'island' (Janzen 1968) during an episode of evolution of host resistance by the usual host of the invading species.

Seasonal considerations

A third major area of underlying assumptions is suggested by the idea that, when hosts are not immediately available for reproduction by the seed predator, the population of seed predators is steadily declining. Since tropical vertebrates do not aestivate in any total sense, and since we are not dealing with highly migratory animals in this discussion, I shall take this assumption to be generally valid for vertebrates. Insects, on the other hand, have a general reputation for being sexually inactive and going into hiding during inimical seasons (e.g. those insects that wait in diapause between mast years of temperate zone forest trees, Janzen 1971a). However, in tropical communities, it appears that many phytophagous insects pass the dry season in reproductive diapause, but as otherwise active adults seeking those bits of

moisture and nutrients adequate for survival but not for reproduction (Janzen 1972c). In the deciduous forest under scrutiny in the present study, the seeds of woody plants are for the most part produced during the dry season, and it is therefore the rainy season that is the inimical period for most bruchids. During this season, the adults of many species can be collected while they are visiting flowers for nectar or while they are resting (?) on foliage in shady places. Just by sweeping the understory of one primary deciduous forest site in July (about two months after the rains had started), 16 of the 38 bruchids known for the area (and breeding there in the dry season) were collected in 1971.

The general habitat appears to be highly heterogeneous for these 'overwintering' adults in terms of survivorship. At least one bit of evidence suggests that the 'islands' of highly favourable habitat have local carrying capacities. When one finds a local high density area for a particular bruchid species, the site exhibits the same characteristics of emigration and immigration shown by most islands. For example, at the deciduous forest site in Costa Rica, the adults of the *Acanthoscelides* bruchid that attack the seeds of the mimosaceous shrub *Mimosa pigra* feed on nectar (and pollen?) of the flowers of this plant during the early rainy season, while 'waiting' for the pods to mature in the late rainy season and early dry season. Here, the island is the source of both adult and larval food (and see Janzen 1968). In July of 1971, an isolated bush with a daily crop of about 80 to 110 inflorescences was relieved of all its beetles each morning for three consecutive days. Each day yielded about 300 beetles. The next day yielded about 25 beetles, as did the 5th to the 8th days. This suggests that the bush and its immediate environs had a pool of about 900 adult beetles, that the daily flower crop could hold only about 300 beetles at any one time, and that the immigration rate of beetles to the bush was about 25 per day. On the 9th to the 17th days, the beetles were released back onto the inflorescences after capture, with the expected result that the total numbers caught each day increased by about 25 beetles. This beetle can be obtained at a density of about 1 per 800 sweeps with a sweep net in the vegetation surrounding the *Mimosa pigra* bush; one sweep through a *M. pigra* bush generally yields 50 to 100 adult beetles.

Islands

As final comment on the background parameters of seed predator ecology, it should be mentioned that the generalities suggested in the previous paragraphs are not expected to hold on real islands in many cases. Tropical island vegetation tends to have the low plant diversity and the poverty of species characteristic of temperate zone habitats, and in my opinion for much the

same reason; the seed predator guild (and foliage feeder guild) is ineffective at breaking up the pure stands of the best competitors. Major parts of the seed predator guild are absent on tropical islands through the difficulty of immigration (e.g. the absence of terrestrial vertebrates from Puerto Rico, Janzen 1972b) and through the difficulty of maintaining a population where there are few alternate hosts (e.g. to provide nectar for adults during the wet season) or alternate habitats. It is also not helpful that the host density is so low and the habitats are so monotonous that in bad years no seed may be produced by a given species of tree.

Biological control

The study of the ecology of the interactions of tropical plants and the animals that eat them is still at an embryonic level. Further, in trying to understand the relevance of field studies, such as those briefly discussed above, to the biological control of pests in agriculture, we are put in the uncomfortable position of trying to expect the unexpected, as Charles Elton has put it. These pious disclaimers notwithstanding, it may be worthwhile to enumerate a few considerations for biological control that the study of tropical seed predators and defoliators has brought to mind.

Perhaps foremost is the idea that tropical woody plants, occurring at low density as they do (on account of their herbivore load, to use Richard Root's term), have their primary external escape mechanism destroyed when planted in high-density plantation systems. Winter is on the side of the temperate zone farmer, and it is perhaps fortunate that he cannot eliminate it (Janzen 1970b) as the dryness of the desert has been eliminated with irrigation. The concentration of host plants by the tropical woody plant agriculturalist means that he is not only asking his biological control agents to depress their prey populations, but asking them to do it when the prey have suddenly had one of their main control mechanisms removed. With herbaceous (annual) crops, there is perhaps less of a problem in this area of cultural control because the farmer at least would appear to have the option of artificially creating a winter and spacing through fallow periods, crop rotation, and interplanting. However, in view of the marginal income level experienced by most tropical subsistence farmers, crop rotation and fallow periods are often not possible under contemporary human population densities and pressures for cash on an immediate basis.

If tropical pest insects turn out to have as few host-specific parasites as do the bruchids studied here, it may in general be extraordinarily difficult to keep a parasite population at a high level in the community while its prey (pest) species fluctuates with the ups and downs of its host plant during the

cropping regime. Maintaining high parasite levels may be even more difficult as the natural vegetation around the field is removed, since the array of alternate hosts for the parasite to choose from will be greatly reduced by this habitat destruction. Finally, if tropical parasites turn out to be as catholic as those reared from the bruchid community, it may be difficult to keep them associated with the pest (prey) species of interest.

The evolution of resistance in crop plants cannot be ignored in any biological control scheme, since it so strongly influences the rates of increase of the pest species on a given crop. We must remember that a large number of the successful tropical crops have been tree crops of cash value to developed countries, but of little or no direct value to either the people producing them or to the majority of the animals in the field-forest community. Here, owing to the long-term nature of the crop, breeding resistant strains hardly fits with the hand-to-mouth economy of subsistence or even with more advanced agriculture. It is also not likely to be very successful in the face of a tropical insect community, the members of which have been playing the chemical coevolutionary game as their way of existence since the upper Cretaceous. With annual crops there might appear to be more hope. However, annual crops tend to be much more edible (to the animal community) than tree crops, since much of their chemical defence has been bred out of them in the process of turning them into crop plants. In breeding for resistance we are putting these compounds back into the plant (instead of on the outside, in the form of insecticides) and it seems unlikely that we can ever reconstitute an edible plant with chemical defences so effective that the plant is as lightly attacked in a field as it is when widely dispersed in a forest or other habitat.

A major component of the biological control of crop pests is the rapid build-up of the parasite or predator on a local outbreak of pests. Temperate-zone habitats appear to abound with parasites and predators that have a high reproductive rate and a behaviour to use it effectively when large amounts of prey are encountered. This is hardly surprising considering the pattern in which their normal prey species become available. However, it appears that tropical parasites and predators have been moulded by natural selection in such a manner that they put much more of their total resources into prey-finding behaviour and physiology, with the result that they are not able to consume an extraordinarily large population of items once found. Again, this is not surprising if one considers the distances that must occur between prey items in natural tropical systems if just the distribution of the prey's host plants is considered. Even if the proper parasite can be found, and even if it can be provided with a large prey population such as may be found in a field, it may be behaviourally and physiologically incapable of responding to a high host density.

As a final comment, I would point out that, over short distances, tropical phytophagous insects seem to be extraordinarily adept at locating their host plants, and at migrating back and forth between alternate habitats. This is true not only of the bruchids mentioned earlier, but also of the insect community as a whole (e.g. Janzen 1973). This means that the increased proximity of fields in large-scale agriculture is likely to accentuate the general problem (even when fields are some distance apart) of a large inoculation of pests starting off the pest population in a field well before the parasite or predator can catch up.

By way of summary, I should like to point out that the previous paragraphs unfortunately support what I consider to be an important fallacy in applied ecology. This is the idea that a general rule, which is nothing more than a statement of central tendency, is necessarily applicable to a specific case and may therefore be used to discourage experimentation in that particular case. We can all think of specific examples arguing for and against each of the general statements made in this paper. The crop plant and its pests are only one of a very small fraction of the plant-insect community whose processes are represented by my generalizations; their specific case may well lie many standard deviations from the mean. Many successful agricultural systems are very atypical of the ecological processes that generate and maintain natural communities (and often because man harvests very different things from the plant than do the other animals in the community). It seems entirely reasonable that there is only one sure way to learn which sets of plants and animals can interact for human profit in the tropics, and that is to try them. Agricultural experiment stations in the tropics are woefully understaffed, ill-equipped and out-of-date. Their personnel are generally not keen pursuers and exploiters of the special features of the tropical agricultural ecosystem. This is not surprising when we realize that their staff are generally products of the educational system of some developed country, with guiding philosophies often oriented towards agricultural ecosystems evolved to deal with the annual pulse of energy provided by the temperate-zone summer. Further, they are coevolved with respect to the economics of the countries that have long profited from that pulsed energy, both directly through yield and indirectly through the evolution of a social system to deal with pulsed yield. Finally, they are guided by governments that demand an agricultural productivity high enough to raise the standard of living for a large number of people to the level seen in the developed countries. What is missing is the active realization by the underdeveloped countries that the developed countries have probably already peaked out on their standard of living, and that one of the major routes to that peak was through exploitation of the produce of the underdeveloped countries. The question then becomes, what country is the underdeveloped country going to exploit to peak its own

standard of living? It often appears that they have chosen to rape themselves. In short, the agricultural system in the tropics is being asked to produce far more than the system can produce, and the tragedy is that its inevitable failure will be blamed on such things as droughts, lack of conscientious effort by applied ecologists, and on political systems, rather than the excess of people, the lack of planning that is generating this excess, and the false expectations generated by using the developed countries as models.

References

- BELL E.A. & D.H. JANZEN (1971). Medical and ecological considerations of L-dopa and 5-HTP in seeds. *Nature, Lond.* **229**, 136-7.
- JANZEN D.H. (1968) Host plants as islands in evolutionary and contemporary time. *Am. Nat.* **102**, 592-5.
- JANZEN D.H. (1969) Seed-eaters versus seed size, number, toxicity and dispersal. *Evolution* **23**, 1-27.
- JANZEN D.H. (1970a) Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501-28.
- JANZEN D.H. (1970b) The unexploited tropics. *Bull. Ecol. Soc. Amer.* **51**, 4-7.
- JANZEN D.H. (1971a) Seed predation by animals. *Ann. Rev. Ecol. Syst.* **2**, 501-8.
- JANZEN D.H. (1971b) Escape of juvenile *Dioclea megacarpa* (Leguminosae) vines from predators in a deciduous tropical forest. *Am. Nat.* **105**, 97-112.
- JANZEN D.H. (1971c) The fate of *Scheelea rostrata* fruits beneath the parent tree: pre-dispersal attack by bruchids. *Principles* **15**, 89-101.
- JANZEN D.H. (1971d) Escape of *Cassia grandis* L. beans from predators in time and space. *Ecology* **52**, 964-79.
- JANZEN D.H. (1972a) Escape in space by *Sterculia apetala* seeds from the bug *Dysdercus fasciatus* in a Costa Rican deciduous forest. *Ecology* **53**, 350-61.
- JANZEN D.H. (1972b) Association of a rainforest palm and seed-eating beetles in Puerto Rico. *Ecology* **53**, 258-61.
- JANZEN D.H. (1973) Sweep samples of tropical foliage insects: effects of seasons, vegetation types, elevation, time of day, and insularity. *Ecology* **54** (in press).
- WILSON D.E. & D.H. JANZEN (1972) Predation on *Scheelea* palm seeds by bruchid beetles: seed density and distance from the parent palm. *Ecology* **53**, 954-9.