OIKOS 54: 185–188. Copenhagen 1989

Vertebrate frugivores and their interaction with invertebrate fruit predators: supporting evidence from a Costa Rican dry forest

Carlos M. Herrera

Herrera, C. M. 1989. Vertebrate frugivores and their interaction with invertebrate fruit predators: supporting evidence from a Costa Rican dry forest. – Oikos 54: 185–188.

Fruit-eating vertebrates may have a significant impact on the population sizes of insect fruit predators that remain inside the fruit after ripening, and it may be predicted that the disappearance or marked reduction of a population of frugivorous vertebrates will lead to a dramatic increase in the population of invertebrate fruit predators. Evidence consistent with this prediction was found for *Amblycerus cistelinus*, a bruchid beetle feeding on the seeds of *Guazuma ulmifolia* in the tropical dry deciduous forests of northwestern Costa Rica. A significant increase in the incidence of *A. cistelinus* from 1972 to 1986 was found at the site where large mammals eating *G. ulmifolia* had been removed in that period, but no change was observed in the same period at the site where some mammalian seed dispersers were present. *G. ulmifolia* plants apparently get two distinct reproductive benefits from their animal mutualists: seed dispersal and a reduction in seed predation through a decrease in seed predator populations.

C. M. Herrera, Estación Biológica de Doñana, E-41013 Sevilla, Spain.

The ripe fruits of vertebrate-dispersed plants are risky places for frugivorous invertebrates living inside them. After ripening, fruits become a target for frugivorous vertebrates that eat and digest fruit, usually killing any enclosed invertebrates in the process. In at least one instance, vertebrate consumers have been shown experimentally to even prefer invertebrate-containing, and hence protein- and lipid-enriched fruit (see Piper 1986), over invertebrate-free ones (Redford et al. 1984). Some behavioural patterns of invertebrate fruit predators may thus be attributable to the distinct selective pressures imposed upon them by the increased mortality risks associated with fruit ripening (Herrera 1984b). These include (1) feeding only on developing, unripe fruits, and leaving them just before ripening (e.g., some tephritid flies, pyralid moths, and bruchid beetles; Southgate 1979, Dreyer 1984, Herrera 1984a, Jordano 1987); (2) altering the physical and chemical properties of the ripe fruit so as to make it relatively undesirable to the vertebrate frugivores (e.g., some moths; Janzen 1983b, Manzur and Courtney 1984, Jordano 1987, Knight 1987); and (3) using the seed coat for protection by living and feeding inside the seed in virtually complete isolation from the external environment (e.g., chalcid wasps eating the seeds of some anacardiaceous fruits; Davatchi 1958, Chung and Waller 1986).

Since these evolutionary responses can only be speculative, the importance of vertebrate predation can be most clearly demonstrated in those instances where invertebrate fruit predators have not developed conspicuous adaptations to escaping the killing action of frugivorous vertebrates of the kind noted above. In these cases, available evidence indicates that vertebrates may be significant mortality factors for frugivorous invertebrates. In an Australian rainforest, Drew (1987) found that frugivorous birds, as a consequence of the destruction of eggs and larvae inside ripe fruits, were the major natural enemies of two fruit-feeding tephritid fly species. Frugivorous birds were also found by Bigler and Delucchi (1981) to be an important source of prepupal mortality for *Dacus oleae*, a tephritid fly, feeding on wild olive fruits. Lamprey et al. (1974) found that ga-

Accepted 28 September 1988

Tab. 1. Infestation rates of *Guazuma ulmifolia* fruit crops by the bruchid beetle *Amblycerus cistelinus* at two Costa Rican dry deciduous forest localities, February 1986.

Tree	Fruits dissected	Fruits infested	%
Santa Rosa:			
1	50	7	14
2	50	1	2
3	50	2	4
4	50	5	10
5	50	5	10
6	50	14	28
7	50	0	0
8	50	4	8
9	50	1	2
10	50	5	10
11	50	2	4
12	46	7	15.2
Total	596	53	8.9
Palo Verde:			
1	81	29	35.8
2	33	24	72.7
A1	35	21	60
A2	76	33	43.4
A3	246	154	62.6
A4	152	97	63.8
Total	623	358	57.5

zelles eating the pods of *Acacia* spp. in Israel and Tanzania were a major cause of mortality for seed-infesting bruchid beetles. These results suggest that fruit-eating vertebrates may have a significant impact on the population sizes of fruit predator species that remain inside the fruit after ripening (Halevy 1974, Lamprey et al. 1974, Drew 1987, Fletcher 1987). Accordingly, the disappearance or marked reduction of a population of frugivorous vertebrates may lead to a dramatic increase in the population of such invertebrate fruit predators. In this note I report evidence consistent with this prediction. The data were obtained in the course of a study on predation patterns by *Amblycerus cistelinus* (Coleoptera: Bruchidae) on the fruits of *Guazuma ulmifolia* (Sterculiaceae) in the dry deciduous forests of northwestern Costa Rica.

The natural histories of *A. cistelinus* and *G. ulmifolia*, as well as their interaction, have been described in considerable detail by Janzen (1975, 1982a, 1983a). The aspects relevant to the present study may be summarized as follows. The only known host plant of *A. cistelinus* in the Costa Rican deciduous forests is *G. ulmifolia* (Janzen 1980). After the fruit ripen on the tree, but before they fall to the ground, the female *A. cistelinus* glue a single egg to each. After hatching, the larva mines through the fruit wall and starts eating the enclosed seeds. Pupation occurs in the core of the fruit. After 1–2 wk in the pupal stage, the adult ecloses and leaves the fruit. A significant proportion of the larval life, and the whole pupal stage of an individual *A. cistelinus* are spent while the *G. ulmifolia* fruit enclosing it is lying on the ground beneath the parent tree, thus exposed to fruit consumers. In the past, these were presumably members of an extinct mammalian megafauna (Janzen and Martin 1982), but present day dispersers in the dry deciduous forests of northwestern Costa Rica are cattle and horses. These eat the fruits accumulated on the ground beneath tree crowns, disperse the seeds, and kill any enclosed *A. cistelinus* larva or pupae.

In February 1986, ripe *G. ulmifolia* fruits were collected from the ground beneath fruiting trees at Palo Verde National Wildlife Refuge and Santa Rosa National Park, Guanacaste Province, Costa Rica. The vegetation at these sites is dry deciduous forest (see Hartshorn 1983 for general descriptions of the sites). In Santa Rosa, fruits were collected from trees growing in the area between the Park Headquarters and the Casona. In Palo Verde, I collected the fruits from trees in the vicinity of the main entrance road, about 2 km NE of the Organization for Tropical Studies field station (2 trees), and near the westernmost boundary of the Refuge, along Apiario road (4 trees). Fruits were kept individually in sealed plastic containers until *A. cistelinus* adults ceased to emerge. All fruits were then dissected to directly determine the incidence of predation by *A. cistelinus* for each fruit sample.

Fruits from Palo Verde had significantly higher infestation rates than those from Santa Rosa (Tab. 1, $P < 0.001$, Mann-Whitney test); the observed ranges do not even overlap (35.8–72.7% for Palo Verde, 0–28% for Santa Rosa). The high incidence of *A. cistelinus* on *G. ulmifolia* fruits in Palo Verde was not an unusual feature of the 1986 season. Fruit samples collected in 1985 in the same general area exhibited similarly high infestation levels (Alarcón 1985).

Janzen (1975) presented a detailed survey of the incidence of *A. cistelinus* in fruits of *G. ulmifolia* in eight localities in northwestern Costa Rica, including Palo Verde and Santa Rosa. The fruits examined for his study had been collected in early March 1972. A comparison of the present results with those of Janzen (Tab. 2) reveals a remarkable change between 1972 and 1986 in the fruit infestation rate at Palo Verde, but not at Santa Rosa. While Santa Rosa infestation rates remained unchanged (range = 2–22%, mean = 12% in 1972; range = 0–28%, mean = 9% in 1986) ($t = 1.0$, P

Tab. 2. Proportion (%) of *Guazuma ulmifolia* fruit crops infested by the bruchid *Amblycerus cistelinus* in 1972 (data from Janzen 1975) and 1986 (present study) at two Costa Rican dry deciduous forest sites. N = number of fruit crops sampled.

Year		Santa Rosa	Palo Verde
1972	Mean±SD (N)	12±6 (13)	18±11 (31)
	Range	2–22	1–45
1986	Mean±SD (N)	9±8 (12)	56±13 (6)
	Range	0–28	36–73

> 0.3), infestation at Palo Verde increased dramatically from 1972 to 1986 (range = 1–45%, mean = 18% in 1972; range = 36–73%, mean = 56% in 1986) ($t = 7.3$, $P < 0.001$).

At the time of Janzen's (1975) study, both Santa Rosa and Palo Verde supported cattle populations that ate *G. ulmifolia* fruits (Janzen 1982a, and pers. comm.). About 4000 cattle were removed from the 10,800 ha of Santa Rosa in 1977–1978, thereby eliminating them from the park (Janzen 1975, and pers. comm.). Free-ranging horses, however, have remained in some areas of the park, including the one where the 1986 fruits were collected. As in Santa Rosa, cattle were also removed from Palo Verde nearly a decade ago (1980), but horses have not been present during this interval. Although I have seen white-tailed deer (*Odocoileus virginianus*) and peccaries (*Tayassu tajacu*) eating fallen fruits, my impression is that they eat only a tiny fraction of the fruit crops; fruits accumulate in large numbers beneath the trees (observations in the dry seasons of 1985 and 1986) in spite of this consumption by deer and peccaries. The essential difference, then, between Santa Rosa and Palo Verde (with regard to the present study) in the period 1972–1986 has been the persistence of some large herbivores (horses) in the former site and its absence from the latter one. At Santa Rosa, horses range widely in brushy and partly forested pastures, and consume *G. ulmifolia* fruits as a regular part of their diet in the dry season (Janzen 1982a). These surrogate dispersal agents "chew [fruits] to a pulp of particle sizes about 4 mm or less in diameter", and do not discriminate between intact and bruchid-infested fruits (Janzen 1982a). Thus horses must cause substantial beetle mortality, and cattle likely have a similar effect. The increased beetle population size at Palo Verde noted in this study can easily be explained by the "extinction" of the major vertebrate dispersal agents within the last decade. Dry forest insect populations may experience important variation in density from year to year (Janzen 1984). The possibility thus remains that 1985 and 1986 were high years, or that 1972 was a low year, for *A. cistelinus* at Palo Verde, independently of the hypothesis proposed here. There are no data to evaluate this possibility.

Janzen (1980) reported that *A. cistelinus* is free from hymenopteran parasitoids (see also Janzen 1977). My much more limited rearings agree with his data (no parasitoids emerged from 411 attacked fruits). The results presented here are consistent with the hypothesis that vertebrate predation plays an important role in regulating the size of the fruit predator populations in those cases where the frugivorous invertebrates remain inside the ripe fruit in a vulnerable state. If vertebrate frugivores do actually regulate the populations of bruchid seed predators, it may then be suggested that the relationship between *G. ulmifolia* and its vertebrate seed dispersers extends far beyond the simple dispersal-food provision mutualism. Vertebrates not only disperse *G. ulmifolia* seeds, but also effectively increase net seed output by keeping populations of seed predators at low levels.

An analogous situation was described by Janzen (1982b) for the bat-dispersed tropical tree *Andira inermis*. Pulp removal by frugivorous bats reduced seed losses to *Cleogonus* weevils in this species. Although the proximate mechanisms are different in the two cases, a feature common to the interactions of *G. ulmifolia* and *A. inermis* with their respective dispersal agents is that the latter not only move seeds away from plants, but also reduce the incidence of seed predators that infest the fruits. The data presented by Halevy (1974) and Lamprey et al. (1974) on the *Acacia*-gazelle-bruchid triad also suggest that gazelles enhance *Acacia* seed output by reducing bruchid populations, and hence predispersal seed predation. In all these examples, the plants are apparently getting two distinct reproductive benefits from their animal mutualists: seed dispersal and a reduction in seed predation through a decrease in seed predator populations. Either of these benefits may account for the evolution of plant traits responsible for the attraction of vertebrates to fruits (nutritious reward contained in the fruit). In other words, the possibility exists that some plants evolved fruit rewards primarily as a way of destroying seed predators via the killing action of vertebrate fruit consumers eating the fruits. Seed dispersal would then ensue as an incidental consequence. The proximate evolutionary mechanism, however, is difficult to envisage unless the number of invertebrate fruit predators arriving at an individual plant in year *n* depends on the number of adult insects produced by the same plant in year *n-1*. If, on the contrary, insect fruit predators ovipositing on a plant's fruit crop have a mixed origin (with respect to individual plants giving rise to them), it would be difficult for any individual to derive a seed predation advantage over conspecifics by evolving a trait that reduces insect fruit infestation. In this case, an individual evolving the advantageous trait (attracting a frugivorous insect predator) would not have its reproductive output much enhanced, because fruit predators raised by conspecifics would continue infesting its fruit crop. In the case of *G. ulmifolia* and *A. cistelinus,* no information is available about how local beetle populations are.

Acknowledgements – The Servicio de Parques Nacionales de Costa Rica authorized fruit collections in Santa Rosa. Observations and collections in Palo Verde in 1985 and 1986 were done while I was teaching in courses of the Organization for Tropical Studies. G. Barrantes, W. Hallwachs, D. H. Janzen, P. Jordano, A. Pereira and F. G. Stiles helped in a variety of ways in Costa Rica, and M. Carrión did the laboratory work. D. H. Janzen, P. Jordano and E. W. Schupp helped to improve earlier versions of this note.

References

Alarcón, C. A. 1985. Depredación en frutos de *Guazuma ulmifolia* en dos sitios, ubicados en la Reserva de Fauna Silvestre de Palo Verde, Guanacaste. – In: Curso 85-2.

Ecología de Poblaciones. Organization for Tropical Studies, San José, Costa Rica, pp. 389–403.

Bigler, F. and Delucchi, V. 1981. Wichtigste Mortalitätsfaktoren während der präpupalen Entwicklung der Olivenfliege, *Dacus oleae* Gmel. (Dipt., Tephritidae) auf Oleastern und kultivierten Oliven in Westkreta, Griechenland. – Z. ang. Ent. 92: 343–363.

Chung, J. C. and Waller, D. M. 1986. Patterns of insect predation on seeds of smooth sumac (*Rhus glabra* L.). – Am. Midl. Nat. 116: 315–322.

Davatchi, G. A. 1958. Etude biologique de la faune entomologique des *Pistacia* sauvages et cultivés. – Rev. Pathol. Vég. Ent. Agric. Fr. 37: 5–166.

Drew, R. A. I. 1987. Reduction in fruit fly (Tephritidae: Dacinae) populations in their endemic rainforest habitat by frugivorous vertebrates. – Aust. J. Zool. 35: 283–288.

Dreyer, W. 1984. Zur Biologie wichtiger Weissdorninsekten und ihrer Parasiten. – Z. ang. Ent. 97: 286–298.

Fletcher, B. S. 1987. The biology of Dacine fruit flies. – Ann. Rev. Ent. 32: 115–144.

Halevy, G. 1974. Effects of gazelles and seed beetles (Bruchidae) on germination and establishment of *Acacia* species. – Israel J. Bot. 23: 120–126.

Hartshorn, G. S. 1983. Plants. Introduction. – In: Janzen, D. H. (ed.), Costa Rican natural history. Chicago Univ. Press, Chicago, pp. 118–157.

Herrera, C. M. 1984a. Selective pressures on fruit seediness: differential predation of fly larvae on the fruits of *Berberis hispanica*. – Oikos 42: 166–170.

– 1984b. Avian interference of insect frugivory: an exploration into the plant-bird-fruit pest evolutionary triad. – Oikos 42: 203–210.

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

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

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

– 1982a. Natural history of guacimo fruits (Sterculiaceae: *Guazuma ulmifolia*) with respect to consumption by large mammals. – Am. J. Bot. 69: 1240–1250.

– 1982b. Simulation of *Andira* fruit pulp removal by bats reduced seed predation by *Cleogonus* weevils. – Brenesia 20: 165–170.

– 1983a. *Guazuma ulmifolia* (Guácimo, Guácima, Caulote, Tapaculo). – In: Janzen, D. H. (ed.), Costa Rican natural history. Chicago Univ. Press, Chicago, pp. 246–248.

– 1983b. Larval biology of *Ectomyelois muriscis* (Pyralidae: Phycitinae), a Costa Rican fruit parasite of *Hymenaea courbaril* (Leguminosae: Caesalpinioideae). – Brenesia 21: 387–393.

– 1984. Natural history of *Hylesia lineata* (Saturniidae: Hemileucinae) in Santa Rosa National Park, Costa Rica. – J. Kansas Ent. Soc. 57: 490–514.

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

– and Martin, P. S. 1982. Neotropical anachronisms: the fruits the Gomphotheres ate. – Science 215: 19–27.

Jordano, P. 1987. Avian fruit removal: effects of fruit variation, crop size, and insect damage. – Ecology 68: 1711–1723.

Knight, R. S. 1987. Coping with seed parasitism: a possible response by *Protasparagus aethiopicus*. – Oikos 48: 15–22.

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

Manzur, M. I. and Courtney, S. P. 1984. Influence of insect damage in fruits of hawthorn on bird foraging and seed dispersal. – Oikos 43: 265–270.

Piper, J. K. 1986. Seasonality of fruit characters and seed removal by birds. – Oikos 46: 303–310.

Redford, K. H., Da Fonseca, G. A. B. and Lacher, T. E. 1984. The relationship between frugivory and insectivory in primates. – Primates 25: 433–440.

Southgate, B. J. 1979. Biology of the Bruchidae. – Ann. Rev. Ent. 24: 449–473.