Avian interference of insect frugivory: an exploration into the plant-bird-fruit pest evolutionary triad

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

It is hypothesized that insect frugivores experience interference from avian seed dispersers while they are on fleshy, bird-dispersed ripe fruits, as a result of exposure to potentially insectivorous birds attracted to fruits. Several predictions emanating from this hypothesis are tested, and verified, for insect frugivores recorded on ripe and unripe fruits in three contrasting Spanish habitats. Frugivorous insects were rare at all sites on ripe fruits and their abundance was inversely related to the abundance of avian dispersers. This pattern was reversed for insects on unripe fruits. Insects tend to occur mostly on unripe fruits where dispersers are abundant, and predominantly on ripe ones where avian frugivores are most scarce. Insect frugivores lacking especial adaptations against bird predation (aphids) were confined to unripe fruits, while those having some discouraging mechanisms (hemipteran bugs) largely predominated on ripe fruits. The finding that avian seed dispersers interfere with insect frugivory supports the notion that bird-dispersed plants, avian seed dispersers and frugivorous insects integrate a complex evolutionary triad in which each component simultaneously interacts with the other two. Further studies on the detrimental effects to plants of insect frugivory are needed before the significance to the plant-disperser mutualism of avian interference to insect frugivores can be correctly assessed.

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Сделано предположение, что насекомые, питающиеся плодами, страдают от распространяющих семена птиц, когда они находятся на мясистых спелых плодах, доступных для потенциальных насекомоядных птиц, привлекаемых плодами. Испытаны некоторые предположения, исходящие из этой гипотезы и проверены для плодоядных насекомых на зрелых и незрелых плодах в 3-х контрастирующих местообитаниях Испании. Плодоядные насекомые редки во всех биотопах на спелых плодах, и их обилие обратно пропорционально обилию птиц-распространителей. Эта зависимость обратна для насекомых на незралых плодах. Насекомые проявляют тенденцию предпостения незрелых плодов с высоким обилием распространителей и предпочтительно зрелые плоды, где плодоядные птицы немногочисленны. Плодоядные насекомые, у которых отсутствуют специальные адаптации против хищничества птиц (тли), скапливаются на незрелых плодах, а те, которые имеют защитные механизмы (клопы) в основном доминируют на зрелых плодах. Данные, что птицы-распространители семян подавляют плодоядных насекомых, поддерживают мнение, что растения, распространяемые птицами, птицы-распространители семян и плодоядные насекомые образуют комплексную эволюционную триаду, в которой каждый компонент самостоятельно взаисодействует с двумя другими. Необходимо дальнейшее изучение вредных воздействий на растения насекомых, питающихся плодами для правильной оценки значения для мутуалистичечких отношений растение-распространитель столкновения птиц и насекомых, питающихся плодами.

1. Introduction

Many plants depend on vertebrates for the dispersal of their seeds (Ridley 1930, van der Pijl 1972) and produce fleshy fruits containing some seeds plus a certain amount of nutritive material ("fruits" hereafter). Dispersal agents usually ingest whole fruits, obtain a reward as a result of digesting the nutritious tissues, and take the seeds away from the parent plant to be later discarded in conditions suitable for germination (Snow 1971, McKey 1975, Howe and Smallwood 1982). In the meantime from ripening to dispersal the fruit is exposed not only to dispersers, but also to a variety of damaging agents which may feed on the nutritive flesh of the fruit, rendering it unattractive to dispersers and/or actually damage the enclosed seeds.

Mechanisms of defence of ripe fruits from pests, as well as their implications in relation to plant-disperser interactions, have been recently discussed by Herrera (1982a), who emphasized the importance of predation pressure on ripe fruits, and its relation to seed disperser supply. These aspects are essential to a better understanding of evolutionary pathways leading to observed patterns of vertebrate seed dispersal. In this paper I formulate a hypothesis concerning the interaction between invertebrate frugivores and avian dispersers, and test a series of derived predictions for three contrasting Spanish habitats representing a broad range of ecological conditions. I will consider the case of surface-feeding insect frugivores alone, leaving aside invertebrates mining through pulp or seeds which are generally invisible from the exterior.

2. The hypothesis and associated predictions

Bird-dispersed plants, avian seed dispersers and frugivorous insects may be seen as components of an evolutionary triad in which each part simultaneously interacts with the other two, and the course of any binary interactive process is largely dependent on the third element of the triad (Herrera 1982a, 1984). Previous studies have emphasized either the plant-disperser (e.g., Snow 1971, McKey 1975) or plant-pest (Janzen 1977, Herrera 1982a, 1984) interactive pairs. The third side of the conceptual triangle, namely the disperser-pest interaction, is the one stressed here, and some patterns resulting from the interaction between avian and insect frugivores are explored. In particular, I wish to test the hypothesis that insect frugivores are subject to interference from avian dispersers while they are on ripe fruits.

Ripe fruits of bird-dispersed plants characteristically advertise themselves with conspicuous colours and fruiting displays (Ridley 1930, van der Pijl 1972), and become a target attracting avian frugivores. Most of these are potentially insectivorous and probably will not disdain an insect found on the fruit surface. The risk to a phytophagous insect of being fed upon by a bird will thus be considerably greater in a ripe fruit than elsewhere, making ripe fruits relatively unprofitable objects of specialization over evolutionary time. The relative safety of a ripe fruit to phytophagous invertebrates will be greater the lower the probability per time unit of the fruit being consumed. All else being equal, this implies that the longer the average time elapsing from ripening to dispersal, the more likely will be the colonization of ripe fruits by insects over evolutionary time (Janzen 1968, Herrera 1982a). This argument applies particularly to insects lacking defensive adaptations against avian frugivores. The vertebrate-attracting nature of fruits must however have favoured the colonization of ripe fruits by phytophagous invertebrates which possess the ability to repell frugivorous birds, hence simultaneously escaping predation and excluding a competitor from a valuable piece of food, in a way similar to that discussed by Janzen (1977) for frugivorous microorganisms. Several testable predictions follow from this hypothesis of insect-disperser interaction:

(1) Surface-feeding insects should be infrequent in nature on ripe fruits of plants dispersed by potentially insectivorous, visually-oriented frugivores like birds.

(2) Invertebrates possessing some kind of discouraging mechanism against birds should predominate among fruit-surface feeding insects. Visual signals should frequently occur.

(3) The incidence of fruit-surface feeding invertebrates should be inversely related to the abundance of avian dispersers.

Unripe fruits are generally more cryptic than ripe ones, and are not fed upon by avian frugivores, thus they may serve to generate several complementary predictions to test the importance of susceptibility of insects to birds implied above:

(4) No inverse relation is to be expected between disperser abundance and incidence of invertebrate frugivory on unripe fruits.

(5) Insect frugivores attacking unripe fruits should tend to leave these as ripening takes place; this behaviour should preferentially be found among insects lacking discouraging mechanisms against birds.

(6) The pulp of unripe fruits usually is of less food value than that of ripe ones because of higher concentration of feeding deterrents or digestive inhibitors (Sherburne 1972, McKey 1979). Pulp-feeding invertebrates should then be expected to be more abundant on ripe than on unripe fruits when dispersers are scarce and do not represent a serious threat to frugivorous insects. The converse, i.e. greater abundance on unripe fruits when dispersers are abundant in the locality, does not necessarily follows from my hypothesis, but its verification would lend strong support to it.

3. Study sites and methods

The potential risk of ripe fruits becoming damaged by insects prior to dispersal is greatest in summer, when invertebrates are most abundant (Thompson and Willson 1978, Thompson 1981, Herrera 1982a), thus I have chosen this period to test the predictions stated above.

The incidence of surface-feeding insects on ripe and unripe fruits was assessed in three widely separated Spanish localities encompassing a broad range of habitat types and ecological conditions. The north-ernmost site, located in the Pyrenees, was the silver fir-dominated (*Abies alba* Miller) mountain forest with sparse broad-leaved trees (*Fagus, Fraxinus, Sorbus, Tilia*) found in the Selva de Oza (Hecho, Huesca pro-vince), at 1050 m a.s.l. Fruit-producing plants are mainly understory herbs and shrubs very patchily distri-buted in the forest, being mostly found in clearings, forest edges and river banks. The vast majority (95%) of local bird-dispersed species mature their fruits in summer (Tab. 1).

The other two sites are located in Andalusia, the southernmost Spanish region. One of them was the Roblehondo area, in the Sierra de Cazorla mountain range (Jaén province), at 1350–1450 m a.s.l. It is veg-etated by open pine forest (*Pinus nigra* Arnold) with a sparse understory of juniper (*Juniperus oxycedrus* L., *J. phoenicea* L.) and thorny shrubs (*Berberis, Crataegus, Rosa*) (see Herrera and Jordano 1981 for further de-tails). A substantial fraction (63%) of local bird-dis-persed plants fruit in summer (Tab. 1). The second An-dalusian site was a dense mediterranean sclerophyllous scrubland on fertile alluvial soils of the Guadalquivir valley lowlands, near El Viso (Sevilla province), at 100 m a.s.l. *Pistacia lentiscus* L., *Myrtus communis* L. and *Olea europaea* L. var *sylvestris* are characteristic species of this scrubland. Only 50% of local bird-dispersed species ripen fruits in summer (Tab. 1) (see Herrera in press a for a more detailed description of this site).

The three localities differ greatly in climate, exemplifying a steep gradient of increasing average an-nual temperature and declining rainfall from Selva de Oza through Roblehondo to El Viso. Selva de Oza is representative of mid-latitude temperate conditions, while El Viso scrubland is a typical warm mediterra-nean-climate habitat. In some sense, Roblehondo has some features of both sites. The percentage of fruit-producing plants which are deciduous declines from 84% in Selva de Oza to 11% in El Viso, in connection with decreasing winter unfavourableness (Tab. 1). The only deciduous species at El Viso are two herbs. The total number of bird-dispersed species present locally is similar at the three sites (18–19) but, as a result of differences in seasonal fruiting patterns, the number of summer-fruiting species varies from 17 (Selva de Oza) to 9 (El Viso), with Roblehondo in an intermediate position (12 species).

In the course of field work with fruiting plants during 1978–1982 involving fruit counts on marked plants, phenological observations, and extensive fruit collec-tions (see Herrera 1982b, c, in press), I counted and collected for identification insects seen feeding on the surface of ripe and unripe fruits. My work implied the examination of most or all local plant species bearing fruit on the day of observation. I always searched for insects on ripe and unripe fruits with similar attention and fruits were examined at close range. Rapid escape reactions (e.g., flying off) in response to my presence were never observed among fruit-feeding insects re-corded, thus I am confident that all individuals present were detected. At Selva de Oza observations and col-lections were done in the period 7–16 September 1981, coincident with the local peak in the diversity and abun-dance of bird-dispersed fruits. At the other two sites, field work took place on separate periods of variable length distributed from 15 July to 15 September in 1979 to 1982. In Roblehondo this period encompasses the local peak of fruit diversity (early September), while in El Viso it occurs nearly one month later (Herrera in press).

To evaluate disperser abundance, avian populations were sampled by means of mist-netting at El Viso and Roblehondo. Nets were operated at irregular intervals during July-September of 1979–1981, and record was kept of total catch effort (net-hours) on every netting

Tab. 1. Summary of relevant features of the three study localities.

Locality	Habitat type	Latitude	Elevation (m)	Average annual temperature (°C)	Bird-dispersed plants		
					Total species	Percent[a] deciduous	Percent[b] fruiting in summer
Selva de Oza	Fir forest	42°12′N	1050	9.9	19	84.2 (80.0)	94.7
Roblehondo	Highland pine forest	37°57′N	1350	12.3	19	63.2 (61.1)	63.2
El Viso	Mediterranean scrubland	37°26′N	100	17.5	18	11.1 (0)	50.0

a. In parenthesis, after excluding herbs.
b. Period 15 July–15 September.

day. Of all birds captured, the number of individuals corresponding to legitimate seed disperser species was expressed in relation to netting effort, and these figures used subsequently as estimates of disperser abundance. Criteria used to categorize bird species and further methodological aspects may be found in Herrera and Jordano (1981), Jordano (1982) and Herrera (in press).

4. Results

4.1. Insect frugivores

A list of insects found feeding on ripe and unripe fruits, and of plants involved, is presented in the Appendix and summarized in Tab. 2. Frugivorous insects belong to the Tettigoniidae, Aphidae and several heteropteran families. Insect frugivores on ripe fruits are dominated by heteropteran bugs at all sites (49 out of 53 individuals; 92%), while their relative significance is far smaller in the case of unripe fruits (507 out of 868; 58%). Cydnidae (a single species restricted to El Viso), Pentatomidae and Coreidae are the heteropteran families contributing most individuals. Aphids were never detected on ripe fruits, while they numbered hundreds on unripe ones.

Tettigoniid grasshoppers chewed pulp and seeds when feeding on fruits. Aphids are sap-feeders and were sucking pulp juices when feeding on fruits. In the case of bugs it was difficult to ascertain whether they were sucking pulp juices or feeding on seed contents.

Very often pulp thickness exceeded mouthparts' length and seeds were out of reach to bugs. The frequent observation of juiceless, shrivelled fruits after hemipteran attack further supports pulp-feeding, but the relative incidence of hemipterans on pulp and seeds cannot be determined at present.

The abundance of surface-feeding invertebrates on ripe fruits was extremely low at all sites. Only 29 individuals were recorded in Roblehondo and El Viso altogether in four summer seasons of field work. One insect individual was found per every about 15000–30000 ripe fruits examined in these sites. The small sample of feeding records available for the southern sites is an unavoidable consequence of the rarity of insects on ripe fruits and is thus in itself a result of the present study.

With frequencies of occurrence as low as those found in the field, accurate counts of fruits examined (necessary to refer insect frugivory rates to number of fruits) would have involved a vast amount of work. Instead, I have referred insect abundance to sampling effort units. Effort has been considered in terms of man-days, i.e. the number of days spent in the field on which I was involved in fruit counts, fruit collections and/or phenological observations. Total sampling effort was 5 man-days in Selva de Oza, 31 in Roblehondo and 27 in El Viso.

In absolute terms, the number of insect species and individuals found in ripe fruits is greater in Selva de Oza than in either of the two southern sites (Tab. 2). When figures are expressed in relation to sampling effort, dif-

Tab. 2. Summary of insect feeding records on ripe and unripe fruits of bird-dispersed plants at the three study sites. See the Appendix for a detailed list of plant and insect species involved. Figures shown are numbers of individuals and species (in parentheses).

	Selva de Oza		Roblehondo		El Viso	
	Ripe	Unripe	Ripe	Unripe	Ripe	Unripe
Orthoptera:						
Tettigoniidae			4 (2)			1 (1)
Heteroptera:						
Cydnidae					3 (1)	450 (1)
Pentatomidae	17 (7)	1 (1)	8 (4)	14 (3)		6 (1)
Acanthosomatidae	4 (1)					
Coreidae	1 (1)		8 (2)	17 (2)	5 (1)	8 (1)
Rhopalidae	1 (1)			1 (1)		
Lygaeidae				8 (1)	1 (1)	2 (1)
Miridae	1 (1)					
Homoptera:						
Aphidae[a]				10 (1)		350 (2?)
TOTAL	24 (11)	1 (1)	20 (8)	50 (8)	9 (3)	817 (7)
Individuals/man-day	4.80	0.20	0.70	1.61	0.33	30.26
Species/man-day	2.20	0.20	0.26	0.26	0.11	0.26
Percent of total found on ripe fruits	96.0		28.8		1.1	

a. Fruit-feeding aphids were tended by ants (*Crematogaster scutellaris* Oliv. in Roblehondo, *Tapinoma nigerrimum* Nyl. in El Viso) in all cases recorded.

ferences become much more extreme, as collecting effort in Selva de Oza was about one sixth of that at other sites. Extreme localities (Selva de Oza and El Viso) display a 20-fold variation in species/man-day and a 15-fold variation in individuals/man-day (Tab. 2). Roblehondo occupies an intermediate position between the other two sites, with figures relatively closer to those of El Viso. Interhabitat variation in the abundance of insects on ripe fruits is far greater than variation in the number of fruit species locally available. On the other hand, average ripe fruit density for the habitat in mid-September (all species combined) is nearly one order of magnitude higher in El Viso than in either of the other sites. This results from more numerous rare species, greater patchiness of fruit-producing plants, and lower average within-plant fruit densities, in the latter two habitats (Herrera in press, unpubl.). The observed variation in insect abundance is not therefore the result of variation across sites in abundance and diversity of ripe fruits available. Insects on ripe fruits are scarcest precisely at the site where ripe fruits are most abundant.

Interhabitat variation in the incidence of insects on unripe fruits contrasts sharply with that exhibited by insects on ripe fruits. The number of species recorded/man-day is closely similar at the three sites (0.20–0.26), and individuals/man-day increase abruptly from Selva de Oza through Roblehondo to El Viso (Tab. 2), just the opposite of the pattern found for insects on ripe fruits. The abundant occurrence of ant-tended aphids and the cydnid bug *Sehirus melanopterus* H.-S., are responsible for the high incidence of insect frugivores on unripe fruits in El Viso (see Appendix).

As a result of the opposed abundance patterns across sites shown by insects on ripe and unripe fruits, the fraction of total individuals at each site recorded from ripe fruits increases steadily from El Viso (1.1%) through Roblehondo (28.8%) to Selva de Oza (96%). Insect frugivores thus tend to concentrate differentially on ripe and unripe fruits at the three sites. While frugivorous insects are mostly found on unripe fruits in El Viso and Roblehondo, they virtually ignore them in Selva de Oza in favour of ripe ones.

The higher abundance of insects on unripe fruits relative to ripe ones in El Viso and Roblehondo must be taken as an indication that (1) insects tend to set themselves preferentially on unripe fruits, largely ignoring ripe ones, or (2) insect frugivores leave unripe fruits when these approach maturity. The case of *Sehirus melanopterus* in El Viso illustrates the first mechanism; on plants of *Osyris quadripartita* with ripe fruits abundantly available they invariably concentrated on unripe ones. Actual retreat is nicely exemplified by aphids. They were never seen on ripe fruits, leaving the fruits of *Rhamnus alaternus, R. lycioides* and *Rubus ulmifolius* shortly before ripening of their host fruits: tending ants transported them to unripe fruits nearby, generally on the same infructescence. Similar behaviour was observed among ants tending aphids on unripe fruits of

Rhamnus myrtifolius Willk. in a locality of the Sierra de Cazorla a few kilometers away from Roblehondo, suggesting that it is widespread among ants which tend aphids on fruits.

4.2. Avian frugivores

Abundance of avian seed dispersers was assessed in Roblehondo and El Viso by mist-netting. Nets were operated on 21 and 7 d, respectively, in the period 15 July—15 September. Averages ($\pm$ SD) of daily capture rates of legitimate avian dispersers were 28.6 $\pm$ 23.9 and 56.9 $\pm$ 26.2 birds/100 net-hours in Roblehondo and El Viso, respectively, and the difference is statistically significant (t = 2.71, P = 0.012). Most captures of avian dispersers in El Viso during the summer study period corresponded to autumn migrant passerines (mainly *Ficedula hypoleuca* Pall., *Phoenicurus phoenicurus* L., *Sylvia borin* Bodd., *S. communis* Lath.; see Herrera in press a). These birds efficiently removed fruit crops shortly after ripening (Herrera in press). Autumn migrants were much scarcer in Roblehondo, both in absolute and relative terms. At this site, individuals of resident species (mainly *Erithacus rubecula* L., *Sylvia atricapilla* L. and *Turdus merula* L.) were the most significant seed dispersers of summer-fruiting plants (Herrera and Jordano 1981, Herrera unpubl.).

Netting could not be carried out in Selva de Oza. Visual counts, both within and outside habitat patches containing fruiting plants, unequivocally showed that avian frugivores were extremely scarce there. Their abundance certainly was at least one order of magnitude lower than in Roblehondo. Not a single instance of fruit-feeding by birds was observed in the course of one week in the field. By the dates of my visit to Selva de Oza, autumn bird migration, involving many frugivorous species, is near its peak in southern Europe (Herrera 1974, Ferns 1975, Torres and León 1979, Thomas 1979, Jordano 1981, 1982). Despite this, a single individual of a migrant frugivore (*Ficedula hypoleuca*; see e.g. Jordano 1982, Herrera in press) was observed (taking insects, not fruits) in a week in Selva de Oza. The scarcity of avian frugivores at this site certainly accounts for the common observation of large numbers of rotting ripe fruits on the ground beneath fruiting bird-dispersed plants (e.g., *Lonicera xylosteum, Sambucus racemosa* L., *Rhamnus alpina*).

5. Discussion

5.1. The interaction between avian and insect frugivores

Results presented above are consistent with predictions stated earlier in this paper and clearly support the hypothesis of avian interference to insect frugivory. Insects were rare on ripe fruits at all sites (prediction 1), and their abundance was inversely related to the abun-

dance of avian dispersers (3). No inverse abundance relation was found between insects on unripe fruits and avian frugivores (4). Insects tend to occur mostly on unripe fruits in places where dispersers are abundant, and predominantly on ripe ones where avian frugivores are scarce (6). Although I have used an unquantified assessment of bird abundance in Selva de Oza (but see below), predicted patterns which depend on an evaluation of bird abundance still persist after excluding this site and considering Roblehondo and El Viso alone (Tab. 2). Aphids, which lack visual or chemical discouraging signals against birds, never occurred on ripe fruits and were carried by tending ants to unripe fruits when host fruits approached maturity (5). The incidence of heteropteran bugs also decreased from unripe to ripe fruits but they were, by far, the most important group of insect frugivores on ripe fruits. Some of the bug species recorded (*Spilostethus pandurus* Scop., *Sehirus melanopterus, Carpocoris mediterraneus* Tamanini) are conspicuously patterned in black and red, as is usual among aposematic insects (Cott 1940). At least *Dolycoris baccarum* L., *S. pandurus* and species of *Palomena, Carpocoris, Acrosternum* and *Gonocerus* possess specialized glands producing secretions which are potentially harmful or distasteful to avian predators (Baggini et al. 1966, Scudder and Duffey 1972, Herrera pers. obs.). In experimental conditions, birds reject toxic hemipterans (Sillén-Tullberg et al. 1982). These observations are consistent with predictions (2) and (5).

Ripe fleshy fruits seem but marginal food substrates for bugs, the principal insect frugivores in the habitats studied. In support of this view are the extremely low frequencies of occurrence on ripe fruits and the broad variety of host plants and plant parts reported for some of the species I found on ripe fruits (Gómez Menor 1956, Al-Ali 1977, Chinery 1976, Herrera pers. obs.). In Roblehondo, for instance, *Carpocoris mediterraneus* was very abundant on inflorescences of *Lavandula latifolia* Med., *Cirsium vulgare* (Savi) Ten. and *Eryngium* sp. at times when it was extremely scarce on fruits. I suggest that differences among sites in abundance and diversity of bugs in ripe fruits are largely the outcome of local hemipteran species tending to include ripe fruits in the array of potentially usable foods with greater frequency where the safety afforded to these insects by ripe fruits is greater. Even chemically defended insects have some risk of being killed or injured by unexperienced birds (Jeffords et al. 1979, Järvi et al. 1981, Sillén-Tullberg et al. 1982) such as recently fledged young which are abundant in summer. Observed interhabitat differences in abundance of early autumn migrants are not attributable either to special conditions during my particular study years or to limited period in the case of Selva de Oza. Similar patterns have been documented in previous studies on the basis of longer sampling periods and/or covering other study years (e.g., Herrera 1974, Purroy 1975, Torres and León 1979, Jordano 1982). Differential abundance of early autumn migrants is the result of (1) habitat-type selection by migrants, which become scarcer with increasing elevation, and (2) broad geographical patterns in the Iberian Peninsula affecting their migratory pathways; migrant abundance increases to the south and to the west of the Peninsula (Bernis 1962, Herrera in press, unpubl.). Early autumn migrants are the main summer seed dispersers in southernmost Europe (Jordano 1981, 1982, Herrera in press a), hence differential abundance of seed dispersers among sites is dependent on geographical and habitat-specific features, and present conditions most likely have prevailed during sufficient time to give rise to a shift in food choice among generalist hemipterans.

5.2. Implications to plants

Implications to fruiting plants of avian interference to insect frugivory documented in this paper obviously depend on the actual significance to the plants of insect frugivory. The extent of actual damage to ripe fruits (and hence the detrimental effect on the parent plant) caused by insects recorded in this study are not yet known. Some detrimental effect on the plant is however to be expected from the activity of insects which destroy pulp and seeds (tettigoniid grasshoppers), impair the attractiveness of the pulp (pulp-feeding bugs), or damage the seeds (seed-feeding bugs). Any impairment in the attractiveness of the pulp, the part of a ripe fruit designed to play an attractive role to seed dispersers, would most likely decrease the chance of seed dispersal (Janzen 1977, Herrera 1982a, M. I. Manzur pers. comm.). It may then tentatively be suggested that an adequate supply of avian seed dispersers seems essential not only to the short-term dispersal of seeds, but also to the long-term maintenance of fruits without a need for defence mechanisms against pests, as suggested by Herrera (1982a).

On the other hand, observations and collections during daytime may not reflect adequately the intensity of fruit predation if nocturnal predation also occurs. Diel changes in the abundance of surface-feeding insects on ripe fruits should indeed be expected from my hypothesis of avian-insect interference. Ripe fruits would become safe places to insects at night, when avian frugivores are inactive, and there is evidence in support of nocturnal insect frugivory (Denslow and Moermond 1982, D. Janzen pers. comm.). Hemipteran bugs have been observed shifting from ripe to unripe fruits of *Rubus caesius* shortly after sunrise (J. A. Amat pers. comm.). Further studies are clearly needed before the implications to the plant-bird mutualistic system of avian interference to insect frugivores can be correctly assessed.

Appendix. Records of insects found feeding on ripe and unripe fruits of bird-dispersed plants at the three study localities, and number of individual insects involved.

Plant species	Insect species	Number of individuals	
		On ripe fruits	On unripe fruits
SELVA DE OZA:			
Actaea spicata L. (Ranunculaceae)	*Palomena prasina* L. (Pentatomidae)	1	
Arctostaphylos uva-ursi (L.) Sprengel (Ericaceae)	*Piezodorus lituratus* F. (Pentatomidae)	2	
Atropa belladonna L. (Solanaceae)	*Holcostethus* sp. (Pentatomidae)	2	
Lonicera xylosteum L. (Caprifoliaceae)	*Carpocoris fuscispinus* Boh. (Pentatomidae)	1	
	Deraeocoris ruber L. (Miridae)	1	
	Dolycoris baccarum L. (Pentatomidae)	1	
	Elasmostethus interstinctus L. (Acanthosomatidae)	4	
	Gonocerus sp. (Coreidae)	1	
	Holcostethus strictus F. (Pentatomidae)	1	
	H. sp. (Pentatomidae)	4	
	Palomena prasina L. (Pentatomidae)	2	
Rhamnus alpina L. (Rhamnaceae)	Unidentified Pentatomidae	1	
Rubus caesius L. (Rosaceae)	*Corizus hyoscyami* L. (Rhopalidae)	1	
R. ulmifolius Schott (Rosaceae)	*Palomena prasina* L. (Pentatomidae)	1	
	Piezodorus lituratus F. (Pentatomidae)		1
Solanum dulcamara L. (Solanaceae)	*Holcostethus sphacelatus* F. (Pentatomidae)	1	
ROBLEHONDO:			
Berberis hispanica Boiss. & Reuter (Berberidaceae)	*Ephippigerida zapatari* Bol. (Tettigoniidae)	2	
Daphne laureola L. (Thymelaeaceae)	*Dolycoris baccarum* L. (Pentatomidae)	3	
	Carpocoris fuscispinus Boh. (Pentatomidae)	2	
D. gnidium L. (Thymelaeaceae)	*C. mediterraneus* Tamanini (Pentatomidae)	1	4
	Spilostethus pandurus Scop. (Lygaeidae)		6
Lonicera etrusca Santi (Caprifoliaceae)	*Gonocerus acuteangulatus* Goeze (Coreidae)	1	
Paeonia broteroi Boiss. & Reuter (Paeoniaceae)	*Ephippigerida zapatari* Bol. (Tettigoniidae)	1	
	Antaxius kraussi Bol. (Tettigoniidae)	1	
	Palomena prasina L. (Pentatomidae)		6
Pistacia terebinthus L. (Anacardiaceae)	*Gonocerus acuteangulatus* Goeze (Coreidae)		2
Prunus mahaleb L. (Rosaceae)	*Palomena prasina* L. (Pentatomidae)		1
Rubus ulmifolius Schott (Rosaceae)	Unidentified Aphidae		10
	Carpocoris fuscispinus Boh. (Pentatomidae)	1	
	Coreus marginatus L. (Coreidae)	7	13
	Coryzus hyoscyami L. (Rhopalidae)		1
	Gonocerus acuteangulatus Goeze (Coreidae)		2
	Holcostethus strictus F. (Pentatomidae)		3
	H. vernalis Wolff (Pentatomidae)	1	
	Spilostethus pandurus Scop. (Lygaeidae)		2
EL VISO:			
Daphne gnidium L. (Thymelaeaceae)	*Spilostethus pandurus* Scop. (Lygaeidae)	1	2
Osyris quadripartita Decne (Santalaceae)	*Odontura spinulicauda* Rambur (Tettigoniidae)		1
	Sehirus melanopterus H.-S. (Cydnidae)	3	450
Rhamnus alaternus L. (Rhamnaceae)	Unidentified Aphidae		250
	Acrosternum heegeri F. (Pentatomidae)		2
	Gonocerus insidiator Fabr. (Coreidae)	2	5
R. lycioides L. (Rhamnaceae)	Unidentified Aphidae		100
	Acrosternum heegeri F. (Pentatomidae)		4
	Gonocerus insidiator Fabr. (Coreidae)	3	3

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