

## APOSEMATIC INSECTS AS SIX-LEGGED FRUITS: INCIDENTAL SHORT-CIRCUITING OF THEIR DEFENSE BY FRUGIVOROUS BIRDS

Fruits of bird-dispersed plants ("fruits" hereafter) are conspicuous when ripe; conspicuousness has evolved in connection with visually oriented mutualistic frugivores which disperse seeds (Ridley 1930; van der Pijl 1982). In addition to conspicuousness, fruits have evolved further attributes to attract their mutualistic consumers (abundance, nutritional reward in the pulp), but many plants produce ripe fruits that have a variety of secondary compounds (poisons, digestion inhibitors) in the pulp (Herrera 1982 and references therein). These substances presumably defend the fruit from frugivores that do not disperse seeds (microorganisms, insects, seed-damaging vertebrates) and perhaps also "filter out" potential dispersal agents on the basis of differential tolerance of secondary compounds (Janzen 1978, 1979; Herrera 1982). These toxic fruits are frequent in most habitat types and are eaten by frugivorous birds (Rowan 1967; Kear 1968; Herrera 1982, unpubl.). This is consistent with some direct and indirect evidence suggesting greater than average toxin tolerance of frugivorous species (Janzen 1978; Pulliainen et al. 1981; Eriksson and Nummi 1982; Herrera 1982, 1984a; Walker 1983).

Aposematic insects signal to potential consumers an objectionable condition arising from the possession of noxious or disagreeable substances (Cott 1940; Eisner 1970; Pasteels et al. 1983). Conspicuousness has evolved here as a way of avoiding predation. Although their chemical defenses do not make them entirely safe from all kinds of avian predators (Calvert et al. 1979; Fink and Brower 1981; Fink et al. 1983), these insects are usually avoided by insectivorous birds (Pasteels et al. 1983). Therefore, toxic ripe fruits of some bird-dispersed plants share with aposematic insects some essential attributes in addition to toxicity. Both are self-advertising structures that use a visual communication channel. In both cases, color and patterning are essential cues to identification by consumer organisms. Furthermore, their respective success (dispersal of enclosed seeds, and escape from predators) similarly depends on appropriate visual signaling and accurate identification by potential consumers. Significantly, in both fruits and aposematic insects, conspicuousness is often enhanced by clustering of individual units. This "convergence" is purely incidental, since the ultimate evolutionary basis for conspicuousness and toxicity is completely different in the two cases.

Even heavily frugivorous bird species regularly ingest some amount of animal prey, probably to overcome nitrogen deficiencies in fruit pulp (e.g., Rowan 1967; Foster 1978; Jordano and Herrera 1981; Jordano 1982; Wheelwright 1983). I hypothesize that frugivorous birds may take advantage of the conspicuousness and ease of capture of aposematic insects, thus short-circuiting insect defense. The hypothesis stems from the assumption that these birds are much less suscepti-

ble than insectivores to the defense of aposematic insects because they have a generalized tolerance to a variety of toxins associated with diverse frugivorous diets and because they are accustomed to consuming brightly colored, and in a sense warning, food items without subsequent negative effects, as an attribute inherent in frugivory.

I examined the hypothesis by testing the following predictions: (1) in a given habitat, species of heavily frugivorous birds should eat aposematic insects more often than do nonfrugivores or marginally frugivorous species; (2) species feeding most frequently on toxic fruits should also ingest aposematic insects most often.

Tests were conducted by comparing the incidence of aposematic insects in the diet of locally coexisting passerine bird species (differing in the degree and nature of frugivory) at three southern Spanish, Mediterranean scrubland habitats covering a broad range of elevation (10–1150 m) and vegetational composition (for detailed descriptions of sites, see Herrera 1984c; Jordano 1984). Study periods were January–December 1978–1980, for El Viso; October–January 1978–1982, for Cazorla; and January–December 1981–1982, for Hato Ratón. Diet composition was studied by examining fecal samples from mist-netted birds. Fecal samples were obtained by flushing the digestive tract with a 1% sodium chloride–water solution. Feces were collected on filter paper and air-dried immediately for storage. Prior to analysis, they were soaked for 24 h. Each sample was examined individually and the remains were sorted. The percentage in volume of fruit remains other than seeds (usually fruit skins) was estimated visually to the nearest 10%. Fruit remains were identified according to species by microscopical examination of skin fragments and comparison with a reference collection of fruit-skin microphotographs. Exoskeletal fragments were used in insect identification (for further details on methods, see Herrera 1981; Jordano 1981). A total of 3245 fecal samples from 20 bird species were considered in the analyses. For the purpose of this study, species have been characterized by average volume of fruits in fecal samples; total number of fruit species recorded; proportional occurrence of toxic fruit species; and proportional occurrence of aposematic insect prey. At each locality, bird species for which I examined fewer than 10 fecal samples, or that forage mostly away from tree and shrub foliage, were excluded from the analyses.

Aposematic insects most commonly identified in fecal samples were *Coccinella 7-punctata* L. (Coccinellidae), *Chrysolina americana* L. (Chrysomelidae), and a variety of lygaeid, coreid, and pentatomid bugs. *Coccinella 7-punctata*, a familiar example of aposematic insect (Cott 1940; Pasteels et al. 1983), secretes the alkaloid coccinelline and has been reported to be rejected by insectivorous birds (Cott 1940; Pasteels et al. 1973; Wiklund and Järvi 1982). *Chrysolina americana*, like other species in its genus, synthesizes cardiac glycosides, which are secreted by specialized glands (Pasteels and Daloze 1977; Daloze and Pasteels 1979; Pasteels et al. 1979; Deroe and Pasteels 1982). I was usually not able to determine the species of heteropteran bugs. These included individuals in the genera *Spilostethus* (?) (Lygaeidae), *Gonocerus* (Coreidae), *Carpocoris*, *Palomena* (?), and *Acrosternum* (Pentatomidae). Production of repellents is frequent in these families and genera (Cott 1940; Baggini et al. 1966; Eisner 1970; Scudder and Duffey 1972), and has been reported as effective against birds (Sillén-Tullberg et al. 1982; Wiklund and Järvi 1982). Even in the absence of accurate species

TABLE 1  
FRUGIVORY AND CONSUMPTION OF APOSEMATIC INSECTS IN PASSERINE BIRDS OF  
THREE SOUTHERN SPANISH HABITATS

SPECIES	N	FRUITS			OCCURRENCE OF APOSEMATIC PREY (%)†
		Average Volume (%)	Species Recorded	Occurrence of Toxic Species (%)*	
<b>Cazorla</b>					
<i>Sylvia atricapilla</i>	100	90.1	13	12.0	46.0
<i>Sylvia melanocephala</i>	15	88.4	7	6.7	6.7
<i>Turdus merula</i>	20	87.6	6	5.0	0
<i>Erithacus rubecula</i>	223	78.3	11	1.8	1.3
<i>Aegithalos caudatus</i>	34	25.8	3	0	0
<i>Parus caeruleus</i>	70	22.7	5	0	0
<i>Parus cristatus</i>	24	9.3	5	0	0
<i>Parus major</i>	15	6.2	4	0	0
<i>Regulus ignicapillus</i>	23	0	0	0	0
<b>El Viso</b>					
<i>Sylvia atricapilla</i>	316	93.3	16	30.1	6.7
<i>Sylvia borin</i>	34	81.2	11	20.6	5.9
<i>Sylvia communis</i>	34	67.8	10	38.2	8.8
<i>Sylvia melanocephala</i>	320	66.6	14	27.8	8.7
<i>Turdus merula</i>	43	54.4	9	16.3	7.0
<i>Erithacus rubecula</i>	140	52.1	8	7.9	.7
<i>Parus major</i>	16	21.3	3	0	0
<i>Phoenicurus phoenicurus</i>	30	10.2	4	0	0
<i>Phylloscopus collybita</i>	31	.7	1	0	0
<i>Ficedula hypoleuca</i>	14	.4	4	0	0
<i>Luscinia megarhynchos</i>	23	.3	2	0	8.7
<b>Hato Ratón</b>					
<i>Sylvia atricapilla</i>	644	85.5	15	17.2	5.9
<i>Sylvia borin</i>	173	81.7	13	48.0	16.8
<i>Sylvia communis</i>	11	70.9	5	54.5	27.3
<i>Erithacus rubecula</i>	289	67.7	8	7.6	2.4
<i>Sylvia melanocephala</i>	236	61.3	13	30.1	19.1
<i>Turdus merula</i>	77	57.4	14	24.7	2.6
<i>Sylvia cantillans</i>	27	53.1	6	33.3	3.7
<i>Phoenicurus phoenicurus</i>	14	48.2	4	14.3	7.1
<i>Sylvia undata</i>	12	38.3	2	0	0
<i>Ficedula hypoleuca</i>	48	34.5	5	12.5	6.3
<i>Luscinia megarhynchos</i>	46	3.7	3	0	4.4
<i>Phylloscopus trochilus</i>	25	.2	2	4.0	4.0
<i>Phylloscopus collybita</i>	84	.1	3	0	1.2
<i>Hippolais polyglotta</i>	34	0	0	0	5.9

NOTE.—Species are arranged at each site in decreasing order of frugivory. *N* is the number of fecal samples examined.

\* Fruit species have been classified as "toxic" on the basis of published information documenting in the pulp of ripe fruits the presence of secondary compounds (e.g., alkaloids, steroid saponins) that are toxic to man and, therefore, may reasonably have a toxic effect on other consumers. See Herrera (1982) for source references and further discussion. Toxic fruit species ingested by birds at study sites are *Tamus communis*, *Arum italicum*, *Solanum nigrum*, *Daphne gnidium*, *Lonicera implexa*, *Lonicera periclymenum*, *Rhamnus alaternus*, *Rhamnus lycioides*, *Asparagus aphyllus*, and *Asparagus acutifolius*.

† This magnitude varies significantly among bird species at all sites ( $G = 152.9$ ,  $df = 8$ ,  $P = 7.0 \times 10^{-9}$  for Cazorla;  $G = 84.6$ ,  $df = 13$ ,  $P = 2.2 \times 10^{-9}$  for El Viso;  $G = 27.0$ ,  $df = 10$ ,  $P = .0026$  for Hato Ratón).

determinations, it thus seemed justified to consider coreid, lygaeid, and pentatmid bugs as aposematic for the purpose of testing the predictions above. Results would not experience substantial modification if all heteropteran feeding records were excluded from the analyses.

The relative importance of aposematic prey varied among sites, with heteropteran prey relatively decreasing, and coleopteran prey increasing, with elevation. The nature of remains found in feces indicated that the birds had swallowed whole individuals of these prey, without discarding any body parts.

Predictions 1 and 2 above are not independent in the particular set of data considered here. A strong association exists in all study sites between the degree of frugivory (average volume of fruit remains in feces) and the frequency of occurrence of toxic fruits (table 1). The overall frequency of occurrence of aposematic prey in feces, all types combined, varies significantly among bird species at all sites (table 1), and the direction of differences observed is the one expected from the first prediction. At all sites, the greatest frequencies of occurrence of aposematic prey consistently occur among a few species occupying the uppermost section of the frugivory gradient. The null hypothesis implied above is that the frequency of ingestion of aposematic prey, as estimated by their occurrence in fecal samples, is the same for all species. Note that this is an extremely conservative procedure, since the probability of detecting any given insect prey type in a fecal sample is, all else being equal, directly related to the proportional importance of insects as a group in the sample, and this magnitude varies greatly, and inversely to degree of frugivory, at all sites.

The frequency of occurrence of aposematic prey is significantly, linearly correlated with the degree of frugivory in none of the sites, with the number of fruit species ingested in El Viso and Cazorla, and with the frequency of occurrence of toxic fruit species in all sites (table 2). Relative magnitudes of correlation

TABLE 2  
CORRELATION COEFFICIENTS BETWEEN FREQUENCY OF OCCURRENCE OF  
APOSEMATIC INSECTS AND THREE VARIABLES RELATING TO FRUGIVORY

HABITAT	<i>N</i>	Average Fruit Volume	No. of Fruit Species <sup>a</sup>	Occurrence of Toxic Fruits
Cazorla	9	.498 <sup>b</sup>	.696* (.172) <sup>b</sup>	.865***
El Viso	11	.571 <sup>b</sup>	.600* (-.138) <sup>b</sup>	.733**
Hato Ratón	14	.466 <sup>b</sup>	.281 <sup>b</sup> (-.306) <sup>b</sup>	.806***

NOTE.—*N* is the number of bird species. Average fruit volume, number of fruit species, and occurrence of toxic fruits are based on data in table 1.

<sup>a</sup> Partial correlation coefficients after removing the effect of occurrence of toxic fruits is in parentheses (see text).

<sup>b</sup> Not significant.

\*  $P < .05$ .

\*\*  $P < .01$ .

\*\*\*  $P < .001$ .

coefficients between frequency of aposematic prey and the other variables are similar at all sites, and the correlation with percentage of occurrence of toxic fruits always yields the highest absolute value. The number of fruit species ingested and the frequency of occurrence of toxic fruits (table 1) are significantly correlated at all sites ( $r = 0.738, 0.880, 0.539$ ;  $P < .05$  or better). When the effect of this correlation is removed, partial correlation between frequencies of aposematic prey and number of fruit species is no longer significant at any site (table 2). This shows that the incidence of toxic fruits in the diet is the single variable (related to frugivory) which is linearly related to the frequency of occurrence of aposematic prey, explaining 53.7%–74.8% of observed variance in this variable. The nature of the relation is the one expected from the second prediction, with bird species ingesting aposematic prey in a frequency directly proportional to their consumption of toxic fruits.

The evidence presented, while clearly supporting the association between the frequent ingestion of aposematic insects and heavy frugivory, is particularly strong in its support of the predicted relation between the ingestion of toxic or distasteful insects and fruits, the most straightforward relation predicted by the hypothesis. Although aposematic insects and toxic plants are often closely associated (Rothschild 1972; Pasteels et al. 1983), the correlation found here definitely is not a result of this association. Aposematic insects recorded in this study were extremely infrequent (a few heteropteran species; see Herrera 1984*b*) or never observed on plants producing toxic fruits. The fact that identical interspecific patterns occur in three contrasting habitats and bird species assemblages, and either at the level of the entire annual cycle (Hato Ratón and El Viso) or in a shorter period (Cazorla), points to their generality in southern Spain. On the other hand, results are not attributable to interspecific differences in foraging methods or microhabitats that could decisively affect encounter rates with aposematic prey. Patterns also hold within smaller subsets of species, such as *Sylvia* species, which are closely similar in foraging tactics and microhabitats yet differ markedly in characteristics of frugivory.

Differences in response to noxious insects by different species of birds have been reported (Brown and Neto 1976; Calvert et al. 1979; Barrows et al. 1980; Fink and Brower 1981; Collins and Watson 1983; Fink et al. 1983). Discernible in the results of some of these studies are patterns resembling those documented here, with species reportedly tolerant of distasteful prey tending to be heavy frugivores (e.g., tanagers, mockingbird). This points to the generality of the phenomenon, and strengthens the notion that frugivory is associated with the acceptance of noxious insects via increased toxin tolerance. From what we now know, any statement regarding the evolutionary avenue(s) for toxin tolerance of frugivorous birds must remain speculative. Frugivorous birds may have evolved toxin tolerance as a consequence of frugivory, but also may have become frugivores because they tolerate the toxins frequently encountered in fruits. If plants and seed dispersers are involved in some sort of coevolutionary interaction, both possibilities may be true. Regardless of the (ultimate) evolutionary origin of the observed relation between frugivory and toxin tolerance, however, the linear relation found between the frequencies of occurrence of aposematic insects and

toxic fruits suggests that the ability to feed on noxious insects is a proximate consequence of an ability to feed on toxic fruits.

The phenomenon documented here reflects an interference situation in a single communication channel used by two transmitter-receiver pairs of organisms (fruit-frugivores and aposematic insects–insectivores). In each of these systems, the signal, and the message it encodes, has evolved in connection with two contrasting ecological relationships (mutualism and predation). The implications of the incidental short-circuiting of the insect defense are manifold, and most of them may be properly assessed only after more detailed studies (e.g., on the ecological and phylogenetic correlates of species-specific differences in susceptibility to noxious substances or learning capacity). It may be suggested, however, that where frugivores are frequent (e.g., in tropical forests and Mediterranean scrublands), the phenomenon should generate selective pressures on aposematic insects, the one participant adversely affected, in the direction of favoring divergence from fruits both in the signal (coloration) and the message (chemical deterrent).

With regard to divergence in coloration, it is interesting to note that most aposematic insects are patterned with stripes or spots of contrasting color (very often the same colors exhibited by fruits), rather than colored as uniformly as most fruits. Furthermore, unicolor aposematic insects are often metallic blue or green, and thus very different from ripe fruits, as pointed out to me by a reviewer. Divergence in chemicals may occur in those instances in which aposematic insects synthesize defensive compounds which depart chemically from plant poisons (Eisner 1970; Pasteels and Daloze 1977; Pasteels et al. 1973; Braekman et al. 1982; Harborne 1982), although there are numerous counterexamples in which insects sequester plant toxins without modification (Duffey 1980; Harborne 1982). The critical aspect to be investigated is, however, whether a relation exists between the frequency of modification of plant toxins by aposematic insects and the degree of similarity between these toxins and those found in ripe fruits. If divergence actually occurs, phytophagous aposematic insects eating plant species (or plant parts) that contain toxins similar to those of ripe fruits in the same habitat should most often modify plant toxins or synthesize new ones. This would be particularly applicable to aposematic insects feeding on ripe fruits. In the only instance of this type known to me in which both plant and insect toxins have been analyzed simultaneously, divergence in chemicals has been demonstrated (Braekman et al. 1982). Finally, if predation from frugivores is to some extent responsible for evolutionary modifications of aposematic patterns, geographical variation in average degree of divergence of aposematic insects from fruits should be directly related to the abundance of toxic fruits and frugivorous birds. Within-habitat, interspecific variation in degree of divergence should be related to the distance from the modal class of food item sizes ingested by regional frugivores.

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