

12 Seed Dispersal of Mimetic Fruits: Parasitism, Mutualism, Aposematism or Exaptation?

Mauro Galetti

Plant Phenology and Seed Dispersal Research Group, Departamento de Ecologia, Universidade Estadual Paulista (UNESP), CP 199, 13506-900 Rio Claro, São Paulo, Brazil

Introduction

Fruits and their seed-dispersers are a classic example of a mutualistic relationship. Seed-dispersers benefit from consuming the nutritious tissues surrounding the seeds, whereas plants benefit from the dispersal of their seeds away from the competition of the parent to newly opened habitat and to places away from the zone of high mortality near the parent plant (Snow, 1971; Howe and Smallwood, 1982).

Several attributes of fruits, including colour, morphology, seed size, phenology and pulp chemistry, are considered plant adaptations to enhance the chances of being eaten by seed-dispersers (van der Pijl, 1982; Janson, 1983; Gautier-Hion *et al.*, 1985). The energy allocated to produce the pulp or aril represents a cost to the plant that probably has no purpose other than to attract seed-dispersers and to protect seeds (Howe, 1993; Mack, 2000). seed-dispersers, on the other hand, also incur costs. Transportation of non-digestible material (seeds) in their guts and exposure to predators while feeding ultimately reduce the rate at which fruit pulp can be processed and

nutrients obtained (McKey, 1975; Levey and Grajal, 1991; Murray *et al.*, 1993; but see Witmer, 1998).

As in most mutualistic relationships, some frugivores and fruiting plants have evolved strategies to overcome these costs without losing the benefits. For instance, some bird species eat fruit pulp and discard the seeds below the parent tree, thereby avoiding the costs of seed ingestion (Levey, 1987). A few plant species have also evolved fruits with no nutritive rewards, presumably deceiving frugivores into swallowing their seeds. These plants enjoy the benefit of dispersal without the cost of pulp production. One such strategy is to hide small fruits and seeds among leaves that are ingested by large herbivores ('foliage is the fruit' hypothesis (Janzen, 1984)). Another strategy is to display colourful seeds resembling fleshy ornithochoric (i.e. bird-dispersed) fruits, so-called 'mimetic fruits' (Ridley, 1930; van der Pijl, 1982). The first strategy is relatively well documented (Janzen, 1984; Quinn *et al.*, 1994; Malo and Suárez, 1998; Ortmann *et al.*, 1998). The second strategy, on the other hand, has been debated since the first monographs on seed dispersal (Ridley, 1930; van der Pijl, 1982), but

very few studies have tested the effectiveness of mimetic fruits in deceiving seed-dispersers (Peres and van Roosmalen, 1996; Foster and Delay, 1998).

In a classic sense, mimicry involves matching colours of edible (in Batesian mimicry) or non-edible species (Müllerian mimicry), to avoid being eaten by predators (Endler, 1981). In the case of mimetic fruits, plants produce seeds that mimic fleshy fruits, thereby facilitating consumption and dispersal of the seed, which provides no nutritive reward to the bird. Fruit mimicry systems apparently share many elements with deceit pollination systems. These include exploitation of naïve consumers, taking advantage of the exploratory behaviour of the animals and use of the signal ordinarily used by truly rewarding systems (in this case, nutritious endocarp) (Dafni, 1984).

Taxonomic Affinities of Mimetic Fruits

Mimetic fruits have been described and discussed by several authors (Ridley, 1930; Corner, 1949; McKey, 1975; van der Pijl, 1982; Williamson, 1982). All of these studies except van der Pijl (1982) focused particularly on *Leguminosae*, primarily because its mimetic species are well known due to their use as jewellery (Armstrong, 1992). We define a 'mimetic fruit' as a brightly coloured fruit or seed with no associated pulp or aril: it consequently does not provide a nutritional reward for potential seed-dispersers. Although such seeds are often termed 'mimetic seeds', I prefer 'mimetic fruits' because the latter terminology makes explicit the model and, hence, the ecological function of the mimicry. My classification is ecological rather than botanical, since different species of plants make use of different structures to mimic fruits. Moreover, we are not concerned with trying to find the probable models for the mimetic fruit, because all species match colour and display patterns common among fleshy-fruited bird-dispersed species.

Mimetic fruits that have a bright visual display are widespread in several non-related

plant families (Colour Plate 1 – see Frontispiece; Table 12.1). At least 21 genera have mimetic fruits with colourful displays, but this phenomenon is particularly common in *Leguminosae* and especially in *Mimosoidea*. Mimetic fruits can be found in herbs (*Gahnia*, *Paenonia*) and vines (*Rhynchosia*, *Abrus*), but are most common in trees (*Abarema*, *Pithecellobium*, *Ormosia*, *Erythrina*, *Harpullia*) (characteristics and family names provided in Table 12.1).

The visual display of most mimetic fruits is a colourful (usually red or red and black or even blue) or black seed against a contrasting colourful background such as yellow, red or orange pods (e.g. *Adenantha pavonina*, *Abarema* spp., *Pithecellobium* spp., *Pararchidendron pruinosum* or *Archidendron grandiflorum*) or other structures (such as in *Paenonia broteroi* (Colour Plate 1)). In the case of *P. broteroi* and other peonies, the non-fertilized ovules are red and contrast with black fertilized ovules (seeds with sarcotesta) immersed in a red carpellary wall (van der Pijl, 1982; C. Herrera, Seville, 2000, personal communication).

Most species with mimetic fruits have long fruiting seasons, which means that fruits are available to seed-dispersers for an unusually long time. Also, the seeds typically have long dormancy periods and several species are rich in secondary compounds that may deter pathogens and other seed predators (Table 12.1). Alkaloids are the main secondary compound found in mimetic fruits, but saponins and flavonoids also occur (Table 12.1).

One of the most well-known and widespread mimetic species is *A. pavonina* (*Leguminosae*, *Mimosoidea*), which has been introduced worldwide. Van der Pijl (1982) fed captive barbets (Capitonidae) *A. pavonina* seeds, but did not mention whether the seeds germinated after gut passage. In addition, Steadman and Freifeld (1999) found six seeds of *A. pavonina* in the crop of the purple-capped fruit-dove *Ptilinopus porphyraceus*, a likely seed-disperser, in Samoa. Ridley (1930) mentioned parrots and pigeons eating *A. pavonina*, but these birds are probably seed predators, not dispersers, of medium or large seeds (see Lambert, 1989). Several long-term studies on diets of neotropical fruit-eating birds have not

Table 12.1. Plant families and genera containing mimetic fruits.

Family	Genus	Species	Life-form	Distribution	Secondary compound*	Colour display
<i>Cyperaceae</i>	<i>Gahnia</i>	<i>sieberana</i>	Herb	Mal.–Austr.	?	Red seed
<i>Euphorbiaceae</i>	<i>Glochidion</i>	<i>sumatranum</i>	Tree	Austr.	Tannin, terpenoids	Orange-red seed
<i>Euphorbiaceae</i>	<i>Margaritaria</i>	spp.	Tree	Pan Tropical	Alkaloids	Metallic blue capsule
<i>Leguminosae</i>	<i>Abarema</i>	spp.	Tree	NTA	?	Blue-white seeds, orange pod
<i>Leguminosae</i>	<i>Abrus</i>	<i>precatorius</i>	Vine	Pan Tropical	Alkaloids	Red and black seeds
<i>Leguminosae</i>	<i>Acacia</i>	<i>auriculaeformis</i>	Tree	Austr.	?	Black seeds, brown pod, yellow funicles
<i>Leguminosae</i>	<i>Adenanthera</i>	spp.	Tree	Austr./Asia/Pacific	Alkaloids	Red or black-red seeds, orange pod
<i>Leguminosae</i>	<i>Archidendron</i>	spp.	Tree	Indomalay, Austr.	Saponin	Black seeds, orange to red pods
<i>Leguminosae</i>	<i>Batesia</i>	<i>floribunda</i>	Tree	NTA	?	Red seeds
<i>Leguminosae</i>	<i>Erythrina</i> †	spp.	Tree	Trop./Subtrop.	Alkaloids	Red or red/black seeds
<i>Leguminosae</i>	<i>Ormosia</i> ‡	spp.	Tree	Pan Tropical	Alkaloids	Red or black/red seeds
<i>Leguminosae</i>	<i>Pararchidendron</i>	<i>pruinatum</i>	Tree	Austr.–Mal.	?	Black seeds, red or orange pod
<i>Leguminosae</i>	<i>Pithecellobium</i>	spp.§	Tree	Neotrop.	Saponin	Black seeds, pink pod
<i>Leguminosae</i>	<i>Rhynchosia</i>	spp.	Vine	Pan Tropical	?	Black-red seeds
<i>Leguminosae</i>	<i>Sophora</i>	<i>secundiflora</i>	Tree	Pan Tropical	Alkaloids	Red seeds
<i>Liliaceae</i>	<i>Allium</i>	<i>tricoccum</i>	Herb	North America	Alkaloids	Black seeds
<i>Ochnaceae</i>	<i>Brackenridgea</i>	<i>nitida</i>	Herb	Pan Tropical	Terpenoids, flavonoids	Black seeds, red sepals
<i>Ochnaceae</i>	<i>Campylospermum</i>	<i>elongatum</i>	Herb	African	?	Black seeds, red sepals
<i>Ochnaceae</i>	<i>Ochna</i>	<i>atropurpurea</i>	Herb	Pan Tropical	Isoflavonid	Black seeds, red calyx
<i>Paeoniaceae</i>	<i>Paeonia</i>	spp.	Herb	M. Europe	Alkaloids	Black seeds, red carpel
<i>Sapindaceae</i>	<i>Harpullia</i>	<i>arborea</i>	Tree	Indomalay	Saponin	Black seeds, yellow capsule

*Secondary compounds found in fruits (reference list sent upon request to author).

†Several species of *Erythrina* have black or brownish seeds (see Bruneau, 1996).

‡Some species of *Ormosia* have black seeds or indehiscent fruits (Rudd, 1965).

§Not all *Pithecellobium* species have mimetic fruits. Also includes *Cajoba*.

Mal.–Austr., Malesia–Australasian; NTA, neotropical Americas; M. Europe, middle Europe.

reported consumption of mimetic fruits (Wheelwright *et al.*, 1984; Loiselle and Blake, 1990; Blake and Loiselle, 1992; Galetti and Pizo, 1996). In fact, very few published studies have reported evidence of avian frugivores consuming seeds of mimetic fruits in the wild (French, 1990; Quin, 1996; Foster and Delay, 1998).

Mammals may eat mimetic fruits, but are probably seed predators. For instance, pig-tailed macaques (*Macaca nemestrina*) were recorded preying upon *Ormosia venosa* seeds on the forest floor in Malaysia (Miura *et al.*, 1997). Peres and van Roosmalen (1996) also recorded spider monkeys preying upon *Ormosia* seeds in an Amazonian forest.

How Did Mimetic Fruits Evolve? Three Adaptive Hypotheses

The parasitism hypothesis

Batesian mimicry involves three agents: the selective agent (the bird), the model (an ornithochoric fruit) and the mimic (the mimetic fruit). All agents affect each other, but only the mimic benefits from this relationship (Endler, 1981). Early studies on seed dispersal hypothesized that mimetic fruits deceive seed-dispersers. Because they provide no benefits for the dispersers and, in fact, take advantage of them, the relationship is parasitic.

The mutualism hypothesis

Peres and van Roosmalen (1996) proposed a hypothesis that mimetic fruits of some species are ingested by terrestrial granivorous birds (tinamous, guans and trumpeters) because the hard-stoned seeds are used as grit to break down other food in the bird's gizzard ('hard seed for grit' hypothesis). The abrasive treatment of the mimetic fruits is hypothesized as essential for their germination. Peres and van Roosmalen (1996) did not provide any evidence that seeds ingested by terrestrial granivorous birds germinate better than seeds ingested by other birds.

The aposematism hypothesis

Aposematism refers to a warning signal (e.g. colours) of animals to advertise unpleasant attributes to avoid predation (Edmunds, 1974). Foster and Delay (1998) proposed that the colour of mimetic fruits is a warning signal of toxicity to seed predators, especially parrots. Some mimetic species (*Ormosia*, *Abrus*, *Sophora*) are well known to contain alkaloids that can kill domestic animals (Tokarnia and Dobereiner, 1997). Alkaloids in seeds, however, are not restricted to mimetic fruits (Herrera, 1982; Cipollini and Levey, 1997).

The seed dispersal system of mimetic fruits is still controversial and poorly tested. We present experimental tests of three hypotheses, using *Ormosia arborea* (*Leguminosae*, *Papilionoidea*) as a focal species.

Material and Methods

Plant species

Ormosia spp. are commonly used in studies on mimetic fruits (McKey, 1975; Peres and van Roosmalen, 1996; Foster and Delay, 1998). The genus contains approximately 100 species that have entirely red, red with a black spot (bicoloured) or entirely black seeds (Rudd, 1965). It is widely distributed and its taxonomy is relatively well studied (Rudd, 1965). Apparently all *Ormosia* species have long fruiting periods (Peres and van Roosmalen, 1996; Foster and Delay, 1998). Our study species, *O. arborea*, occurs in south-east Brazil in forest and *restingas* (Rudd, 1965). In some areas, fruits persist for as long as 36 months (M. Galetti, unpublished data). The fruit is a dehiscent pod, exposing a single red and black seed. Mean seed diameter is 12.85 ± 1.18 mm ($n = 20$). Because accurate information on seed-dispersers of *O. arborea* is lacking, we combined field and captive-animal experiments; we assume that experiments with captive animals can provide important clues to the dispersal of *O. arborea* seeds in the field.

Study Areas

All captive experiments were carried out at Bosque dos Jequitibás Zoo, Campinas, south-east Brazil, and at CRAX, a bird breeding facility specializing in Galliformes, at Contagem, Minas Gerais.

Field experiments were carried out in three areas:

1. Bosque dos Jequitibás, a 10 ha forest fragment in Campinas with a high density of agoutis (*Dasyprocta leporina*).
2. Parque Estadual Intervales, a 50,000 ha Atlantic Forest site near Sete Barras, São Paulo. It hosts one of the highest diversities of birds in the entire Atlantic Forest of Brazil (Aleixo and Galetti, 1997).
3. Estação Ecológica (EE) de Caetetus in Gália west of São Paulo. It has 2100 ha of semideciduous forest, with large populations of large frugivorous birds and mammals.

What Eats *Ormosia* Seeds?

Aviary experiments

We first asked: 'What eats and disperses *O. arborea* seeds?' We offered seeds *ad libitum* to several species of captive birds we thought were likely to consume *O. arborea* seeds in the field. These included large frugivores-granivores (jacutinga, *Pipile jacutinga*, $n = 2$ birds; black-legged guan, *Penelope obscura*, $n = 3$; trumpeter, *Psophia viridis*, $n = 2$; curassows, *Crax fasciolata* and *Crax blumenbackii*, $n = 8$ of each; and solitary tinamous, *Tinamous solitarius*, $n = 8$) and large, canopy frugivores (toco toucan, *Ramphastos toco*, $n = 6$; and bell-bird, *Procnias nudicollis*, $n = 1$).

All birds were housed in large cages and supplied food (fruits and a synthetic diet) *ad libitum* and were in good health. We also offered *O. arborea* seeds to several mammal species (spider monkey, *Ateles paniscus*, $n = 2$; capuchin monkey, *Cebus apella*, $n = 5$; and tapir, *Tapirus terrestris*, $n = 2$) and reptiles (tegu lizard, *Tupinambis meriane*, $n = 5$; and tortoise, *Geochelone carbonaria*, $n = 2$) to observe how the seeds were treated (swallowed, chewed up, spat

out, etc.). These experiments provided qualitative data; quantitative data are not presented because some animals became satiated during the experiments.

Field experiments

To determine *O. arborea* consumers in the field, we watched three fruiting *O. arborea* trees for 60 h (30 h during the dry season and 30 h during the wet season) at EE Caetetus. Because we did not observe any visitors to these trees, we set up five camera traps (Camtrack®) to detect frugivores eating *O. arborea* seeds on the forest floor. One camera was set up below a fruiting *O. arborea* for 4 months at Caetetus, while the others were set up at Parque Estadual Intervales. In total, the cameras were able to detect visits to the seeds of *O. arborea* during 4080 h. All animals that ate *O. arborea* seeds in captivity and that were photographed were assumed to eat *O. arborea* in the wild, even though we did not directly or indirectly (via photography) observe them ingesting seeds.

Testing the Parasitism Hypothesis: Do *O. arborea* Seeds Deceive Avian Frugivores in the Presence of a Putative Model?

If mimetic fruits deceive seed-dispersers, we would expect that birds would not distinguish between the model (rewarding) fruit and the mimetic fruit. In neotropical forests, several plant species produce arillate fruits that may be models of mimetic fruits. These include *Copaifera langsdorffii*, *Copaifera trapezifolia* (*Leguminosae*), *Sloanea* spp. (*Elaeocarpaceae*), *Cupania* spp. (*Sapindaceae*), *Alchornea triplinervia* (*Euphorbiaceae*) and many others (see Galetti, 1996). All experiments were carried out using *C. langsdorffii* (*Leguminosae*, *Caesalpinioidea*) as the model. This bird-dispersed species has black seeds partially covered by an orange aril and a diaspore similar in size to that of *O. arborea* and is eaten by several bird species (Galetti and Pizo, 1996).

Experiment using adult birds

Three pet wild-caught toucans (*R. toco*) and three guans (*Penelope superciliosus*) were housed in separate enclosures (2.5 m × 1.5 m × 1.5 m). Because none was captive-bred and all came from undetermined origins, it is possible that these birds had previous contact with *O. arborea* and its models before capture. The three toucans were chosen from a group of 15 that were living in a large enclosure. All experiments started 1 week after the birds were housed in our small enclosures, which appeared to be sufficient time for acclimatization. All birds were fed bananas and papaya and seemed to be in good health. Feeding trials with birds were conducted in the morning, when the birds were most active. Two experiments were carried out on adult birds. In the first, we offered a dish containing 20 *O. arborea* and 20 *C. langsdorffii* seeds to the three guans and to the three toucans. After 24 h we counted the number of seeds of each type ingested and defecated. After 48 h we repeated the experiment using the same birds. In the second experiment, we used only toucans. We offered each toucan (not all three together, as in the first experiment) 20 *O. arborea* seeds, 20 *C. langsdorffii* fruits (i.e. seed plus aril) and 20 *O. arborea* seeds with transplanted *C. langsdorffii* arils. After 24 h we counted the number of seeds of each type ingested and defecated. The experiment was repeated twice (i.e. 60 seeds of each type were offered to each toucan).

Experiment using naïve birds

Naïve birds are less selective in their diet than adult birds (Barrows *et al.*, 1980), so we predicted that naïve birds would be more easily 'deceived' by mimetic fruits than adult birds. We tested whether *O. arborea* seeds would deceive naïve, captive-born toucans (i.e. if *O. arborea* seeds would be ingested by them). Three captive-bred *R. toco* were housed in separate enclosures. They were fed their normal diet and offered 30 *O. arborea* seeds. We counted the number of seeds swallowed. After

24 h and 48 h we repeated the experiment. After another 2 days, without offering any *O. arborea* we offered *Ormosia* seeds with attached artificial arils made of red plasticine (without smell or taste). The number and type of seeds swallowed were recorded after 3 h. The trials were replicated after 24 and 48 h. After another 2 days, we offered *O. arborea* seeds without arils to determine if the behaviour of the birds had changed.

Field experiments

At EE Caetetus, we placed five stations below the crown of a fruiting *C. langsdorffii* tree. The tree bore thousands of ripe arillate fruits, which were frequently dropped to the forest floor by monkeys and birds. Fallen fruits were avidly consumed by three species of thrushes (*Turdus albicollis*, *Turdus rufiventris* and *Turdus amaurocalinus*) and by white-lipped (*Tajacu pecari*) and collared peccaries (*Tajacu tajacu*). Both peccary species destroy *C. langsdorffii* seeds and thus were considered seed predators.

Stations were spaced 3 m apart. At each station we placed one *O. arborea* seed, three *C. langsdorffii* seeds with attached arils and one *O. arborea* seed with a transplanted *C. langsdorffii* aril. *C. langsdorffii* arils can be easily fitted on to *O. arborea* seeds in such a way that even humans cannot distinguish the difference between *O. arborea* with *C. langsdorffii* arils and *C. langsdorffii* seeds with *C. langsdorffii* arils. The ratio of three model seeds to one mimetic fruit was arbitrary. The stations were checked every 15 min, the number and type of seeds eaten recorded and removed seeds replaced. Sixty-nine replacements were made during 5 h of observations.

Testing the Mutualism Hypothesis ('Hard Seed for Grit' Hypothesis): Do *O. arborea* Seeds Require Abrasive Treatment to Germinate?

The 'hard seed for grit' hypothesis (Peres and van Roosmalen, 1996) predicts that seeds

defecated or regurgitated by birds with non-muscular gizzards (e.g. toucans) would have lower germination rates than those defecated or regurgitated by birds with muscular gizzards (e.g. Galliformes). To test this prediction, all seeds defecated or regurgitated by guans (*Penelope* and *Pipile*) and toucans (*Ramphastos*) in the aviary experiments were collected and tested for germination in the greenhouse. Each seed was sown in vermiculite and watered daily. Control seeds were not defecated or regurgitated but were otherwise treated identically.

Are Red and Black Seeds More Prone to be Eaten by Animals than Black Seeds?

If mimetic fruits of *O. arborea* evolved their conspicuously contrasting colours to attract frugivores, we would predict that red and black seeds are more likely to be eaten than totally black seeds.

Aviary experiments

We offered three captive toucans (*R. toco*) 30 *O. arborea* seeds and 30 *O. arborea* seeds painted completely black with non-toxic black, as described in the first aviary experiment. The painted seeds were left to dry for 24 h before being offered to the birds. We then counted the number of each seed type ingested and defecated, 24 h after offering them.

Field experiment

At Parque Estadual Intervales we set up 29 plots for each treatment. One treatment had 20 *O. arborea* seeds that were painted all black, the second treatment had 20 *O. arborea* seeds in which only the black part of the seed was painted black (to test whether the ink would affect seed predation) and the third had 20 *O. arborea* seeds that were untreated, as controls. Plots were spaced 100 m apart. The number of removed seeds was counted after 40 days. One camera trap was set up to record

frugivore visits to each type of seed ($n = 3$ cameras).

Testing the Aposematism Hypothesis: Do the Colours of *O. arborea* Seeds Reduce Seed Predation by Rodents?

Aposematism is a well-studied phenomenon in insects (e.g. Gamberale and Tullberg, 1998), in which bright colours have evolved as a warning display to predators (usually birds) to reduce the probability of attack (Ritland, 1991). If mimetic fruits evolved colourful seeds as a warning signal of toxicity to seed predators, we would expect that black seeds would be more prone to predation by rodents than would red and black seeds. Note that this prediction is the opposite of that generated by the mutualism hypothesis; rather than focusing on the tendency of brightly coloured seeds to attract dispersers, it focuses on the tendency of these seeds to repel seed predators.

Field experiments

We carried out the experiment in Bosque dos Jequitibás, where agoutis (*Dasyprocta leporina*) are tame and can be observed closely. We set up 30 stations, spaced 100 m apart. At each station we placed one *O. arborea* seed (control) and one *O. arborea* painted completely black. We recorded the number and type of seeds eaten by agoutis after 120 h.

Statistical Analysis

Prior to statistical analyses, all variables were tested for normality and homogeneity of variance. When assumptions of normality and equal variance were not met, the variables were transformed (log transformation for mass and linear dimensions; angular transformations for proportions). If assumptions were still not met, we used non-parametric tests. Categorical data were analysed with χ^2 tests or, when expected values were < 5 , with G tests (Sokal and Rohlf, 1995).

Results

What eats *O. arborea* seeds?

Aviary experiments

In trials with captive animals, *O. arborea* seeds were occasionally swallowed by a small assemblage of birds, including toucans (*R. toco*), guans (*P. jacutinga* and *P. obscura*) and trumpeters (*P. viridis*), but were ignored by bellbirds (*P. nudicollis*), mammals (*T. terrestris*, *C. apella*, *A. paniscus*) and reptiles (*G. carbonaria* and *T. meriane*). Curassows (*C. fasciolata* and *C. blumenbackii*) mandibulated the seeds but did not swallow them.

Field observations

In the wild, we observed white-lipped (*T. pecari*) and collared peccaries (*T. tajacu*) preying upon the seeds of *O. arborea* at EE Caetetus. Both peccaries chewed seeds and spat out the seed-coat. We saw no bird consume *O. arborea* seeds during 60 h of observation.

At Intervales, we recorded in the photographs only agoutis (*D. leporina*, $n = 15$ pictures), tinamous (*T. solitarius*, $n = 5$) and a dove (*Geotrygon montana*, $n = 3$) visiting the fallen seeds of *O. arborea*. Both agoutis and tinamous were classified as seed predators based on captive studies.

Testing the parasitism hypothesis: do *O. arborea* seeds deceive avian frugivores in the presence of its putative model?

Experiment using adult birds

In the first experiment, both toucans and guans preferred *C. langsdorffii* fruits to *O. arborea* seeds (Mann–Whitney U test, $U = 21$, $P = 0.002$). There was no difference between their degree of preference ($U = 52$, $P = 0.23$). Only eight seeds of *O. arborea* were eaten by toucans and five by guans, compared with 79 and 25 *C. langsdorffii* fruits consumed by toucans and guans, respectively.

In the second experiment (in which we offered *O. arborea* seeds, *O. arborea* seeds with

aril and *C. langsdorffii* fruits), there was a statistically significant difference among the three seed types in the number ingested by toucans (Kruskal–Wallis test, $H = 9.02$, $P = 0.009$). Of 120 presentations, adult toucans ingested 13.2 ± 7.5 *C. langsdorffii* fruits, 10.7 ± 3.6 *O. arborea* seeds with aril of *Copaifera* and only 1.3 ± 3.3 *O. arborea* seeds.

Experiment using naïve birds

Naïve toucans consumed significantly more *O. arborea* seeds when only *O. arborea* seeds were offered than did adult, non-naïve toucans (two-way repeated-measures analysis of variance (ANOVA), $F = 19.90$, $P < 0.0001$). After ingesting *O. arborea* seeds with transplanted arils, the toucans rejected bare *O. arborea* seeds and even *O. arborea* seeds with transplanted arils (Fig. 12.1).

Field experiments

In our field experiment, wild birds (*Turdus* spp.) did not ingest any *O. arborea* seeds. They ingested only *C. langsdorffii* fruit (53% of fruits offered, $n = 207$ seeds) and *O. arborea* seeds with transplanted arils (14% of fruits offered, $n = 69$ seeds). The birds strongly preferred *C. langsdorffii* fruits to *O. arborea* seeds with transplanted aril (G test, $G = 16.1$, d.f. = 1, $P < 0.0001$).

Testing the mutualism hypothesis ('hard seed for grit' hypothesis): do *O. arborea* seeds require abrasive treatment to germinate?

We collected 19 *O. arborea* seeds from the faeces of *P. jacutinga*, 20 from *P. obscura* and four from *P. viridis*. *Tinamous solitarius* ingested a few seeds, but we did not find any intact in their faeces. Seeds defecated or regurgitated by captive guans and toucans and the control were planted in a greenhouse and compared (Fig. 12.2).

Eight months after sowing, seeds of *O. arborea* started to germinate. After 13 months, there was a significant difference in per cent germination between treatments and control ($G = 6.4$, d.f. = 2, $P = 0.04$). However, this difference was not the one predicted.

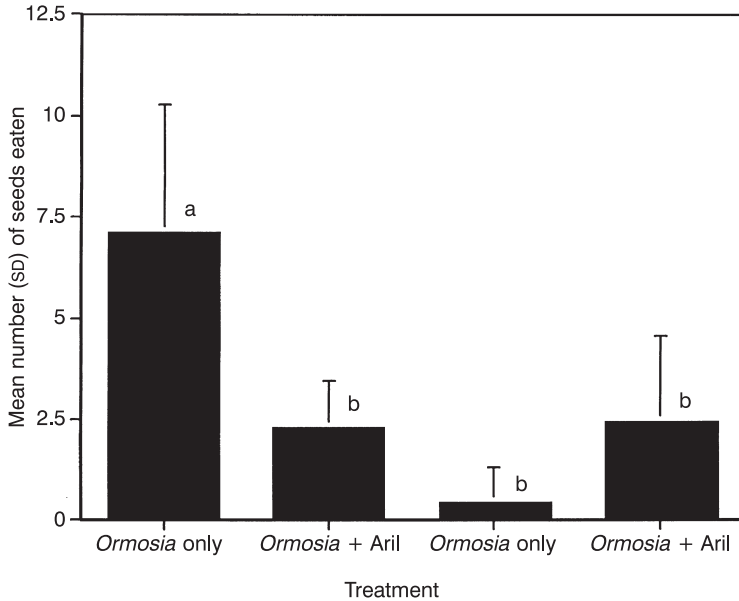


Fig. 12.1. Mean (and standard deviation) of number of *Ormosia arborea* seeds eaten by three naïve toucans (*Ramphastos toco*). Different letters signify statistical differences ($P < 0.05$).

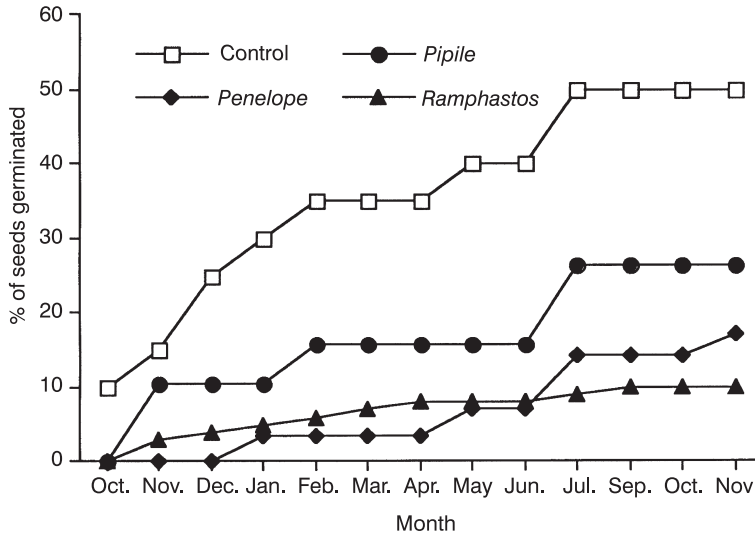


Fig. 12.2. Germination rates of *Ormosia arborea* seeds defecated or regurgitated by three species of birds and the control seeds, which were not ingested by birds. No seeds germinated for the first 7 months after sowing; these months are not shown on the x axis.

In particular, there was no difference in per cent germination among seeds ingested by guans and toucans and, in fact, all ingested seeds had substantially lower per cent germination than control seeds (Fig. 12.2). These results do not support the prediction

that germination of *O. arborea* seeds is higher when passed through the gut of granivorous birds with muscular gizzards (e.g. guans) than when passed through frugivorous birds with non-muscular gizzards (e.g. toucans).

Are red and black seeds more prone to be eaten by animals than black seeds?

Aviary experiments

There was no difference in the number of natural (red and black) and all-black *O. arborea* seeds consumed by toucans (25 all-black seeds versus 26 red/black seeds). This suggests that the colour of *O. arborea* seeds does not enhance seed ingestion by toucans in these circumstances. The influence of seed colour on probability of ingestion may be different in nature, however.

Field experiments

We found no statistical difference in removal of natural *O. arborea* seeds, *O. arborea* seeds painted all black and *O. arborea* seeds with the naturally black part painted black (ANOVA, $F = 0.6$, d.f. = 2, $P = 0.5$). *Ormosia arborea* seeds that were naturally red and black were consumed slightly more often (2.3 ± 2.6 seeds) than *O. arborea* seeds with only the black part painted (1.9 ± 2.7) and *O. arborea* seeds painted completely black (1.4 ± 2.3 , $n = 190$ seeds of each seed type offered).

Testing the aposematism hypothesis: do the colours of *O. arborea* seeds reduce seed predation by rodents?

We found no difference in seed predation levels by agoutis between black-plus-red and all black seeds ($\chi^2 = 12.4$, $P = 0.002$). Sixty-nine per cent of natural *O. arborea* seeds and 79% of *O. arborea* seeds painted all black were preyed upon after 120 h.

Discussion

The experiments described here comprise the first attempt to test alternative hypotheses about mimetic fruits. We caution that the results of experiments using captive birds are tentative because we do not know whether the birds had previous experience with mimetic fruits in the wild. Overall, our results best support the parasitism hypothesis – mimetic fruits deceive avian frugivores – although such

deception is extremely rare in the wild (Foster and Delay, 1998).

The mutualism hypothesis

The mutualism hypothesis ('hard seed for grit' hypothesis) posits that the hard seeds of mimetic fruits are dispersed by terrestrial galliform birds that use the seeds as grit. The abrasive treatment in the birds' gut is presumably essential for seed germination (Peres and van Roosmalen, 1996). Our experiments led us to reject this hypothesis; we did not find a difference in seed germination of *O. arborea* seeds defecated by birds that would or would not be likely to use the seeds as grit. In fact, all seeds from bird defecations had lower germination rates than uningested control seeds. Moreover, we would expect that the contrasting colours of *O. arborea* seeds on the forest floor would attract more dispersers than if they were only black (as proposed by Peres and van Roosmalen, 1996). Again, we did not find any difference in seed removal between black and red/black seeds. Studies on the diet of neotropical Galliformes (Cracidae and Tinamidae) have not reported any species of mimetic fruit in their diet (Erard *et al.*, 1991; Galetti *et al.*, 1996; Yumoto, 1999; Santamaria and Franco, 2000). All large terrestrial cracids (*Crax*, *Mitu*) and tinamids (*Tinamous*) are primarily seed predators of large seeds (Bockerman, 1991; Yumoto, 1999; Santamaria and Franco, 2000). Jacutingas (*Pipile*) and guans (*Penelope*) are more arboreal and are mainly seed-dispersers, but they were never recorded visiting areas with *O. arborea* seeds by our cameras.

The aposematism hypothesis

The aposematism hypothesis was also rejected, at least for large-bodied diurnal rodents (e.g. agoutis), but more experiments using other vertebrates, such as parrots, are necessary. *Ormosia* spp. are rich in quinolizidine alkaloids (Ricker *et al.*, 1999), which may be important in deterring seed predation by rodents and insects (P. Guimarães, M. Galetti and J. Trigo, unpublished data). Other taxa

with mimetic fruits (e.g. *Erythrina*, *Abrus* and *Sophora*) are well known to be toxic to vertebrates and insects (Ramos *et al.*, 1999), but alkaloids are not exclusive to *Leguminosae* with brightly coloured seeds (A. Tozzi, 2000, unpublished data).

The parasitism hypothesis

The only hypothesis supported by our experiments was the parasitism hypothesis. Naïve birds were more frequently deceived by *O. arborea* seeds than were non-naïve birds, as predicted by the hypothesis. In fact, adult toucans rejected *O. arborea* seeds only when we presented an arillated fruit with a mimetic fruit. Because mimetic fruits have a long fruiting season, it is likely that mimetic fruits are more prone to be dispersed during periods of low fruit availability. Several species considered mimetic have long dormancy and their seeds can be attached to the pod for up to 3 years (e.g. *O. arborea*). All of these characteristics are probably adaptations enabling the plant to maximize the period when seeds are available to dispersers (Peres and van Roosmalen, 1996; Foster and Delay, 1998).

Why are *Ormosia* Seeds Colourful?

Although our experiments support the parasitism hypothesis, we suggest that analysis of fruit morphology of the entire genus may provide clues to the evolution of colourful seeds. Fifty species of *Ormosia* occur in the neotropics and 50 others in the Old World (Rudd, 1965). A puzzling aspect of this genus is that even indehiscent species have colourful seeds and one dehiscent species has totally black seeds (Table 12.2). Assuming that species with

abiotic dispersal mechanisms and indehiscent fruits represent the plesiomorphic (ancestral) state of *Papilionoidea* (Janson, 1992), we suggest that seed colour cannot be interpreted as an adaptation to present-day seed-dispersers.

Furthermore, several species of *Ormosia* that occur in flooded forests and have indehiscent fruits are dispersed by water (hydrochory) (Ziburski, 1991; Janson, 1992). Therefore, an evolutionary transition between two passive dispersal modes would be a more parsimonious interpretation than a transition from hydrochoric to endozoochoric syndromes (Janson, 1992; Jordano, 1995). In fact, autochory and hydrochory seem to be the main seed-dispersal syndromes in several mimetic species. Several species with mimetic fruits occur along rivers and have been recorded in studies on water dispersal. Murray (1986) listed two mimetic species (*Abrus precatorius* and *Erythrina variegata*) as capable of long-distance dispersal by ocean currents. It seems astonishing that there is no record of birds dispersing *A. precatorius*, one of the most invasive plants in Florida, USA. *Adenanthera pavonina* is also considered invasive in several islands in Oceania, but we do not have any unambiguous records of birds dispersing viable seeds of this species (only records of gut contents) (Steadman and Freifeld, 1999).

The current worldwide distribution of *Sophora* (which belongs to the same tribe as *Ormosia*), another genus with mimetic fruits, is due to ocean dispersal (Hurr *et al.*, 1999), although *Sophora macrocarpa* is also dispersed by cattle in Chile (R. Bustamante, 2000, personal communication). Most species of *Archidendron* and *P. pruinosum*, also mimetic species, occur along watercourses or in coastal areas (Cowan, 1998a, b). Several species of *Erythrina* occur in flooded areas and are able to float (Bruneau, 1996) and there are scant observations of

Table 12.2. Seed colour, habitat and occurrence of dehiscent fruits in neotropical *Ormosia* (following Rudd, 1965).

	Seed colour			Habitat	
	Red	Black	Red/black	<i>Terra firme</i>	Riverine
Indehiscent	5	0	2	0	5
Dehiscent	8	1	34	18	14

Erythrina being dispersed by birds (C.T. Downs, 2000, unpublished data).

Ecological patterns not linked to adaptive processes from current selection but to phylogenetic constraints may explain the seed colour of some mimetic species. For instance, seed colour in *Erythrina* is highly constrained by phylogeny (Bruneau, 1996). Phylogenetic constraints in several traits of fruit morphology, in fact, has been found to be more common than traits moulded by ongoing effects of natural selection (Herrera, 1987, 1992; Fischer and Chapman, 1993; Jordano, 1995).

We propose that the seed-dispersal system of *O. arborea*, and probably of most *Leguminosae* with mimetic fruits, is a typical case of exaptation. Exaptation represents the secondary use of a trait already present for other (generally historical) reasons (i.e. traits fit for their current role but not designed for it) (Gould and Vrba, 1982). Endozoochorous dispersal of mimetic fruits may certainly occur, but it is an extremely rare event. Despite being a rare event, sporadic dispersal by vertebrates might greatly contribute to fitness of rare species with mimetic fruits.

But what constitutes a rare event in vertebrate seed dispersal? There are few long-term studies on fruit fall to evaluate this question for mimetic fruits. Data for 13 years (January 1987 to January 2000) of seed fall on Barro Colorado Island (Panama) revealed only two seeds of *Ormosia* (one *O. coratti*, one *O. macrocalyx*) away from conspecifics in 200 0.5 m² traps (100 m²) in a 50 ha plot. One seed was found more than 400 m from any *Ormosia* adult and the other 95 m away (S.J. Wright and R. Condit, 2000, unpublished data). The long-distance movements of both these *Ormosia* seeds are probably the result of arboreal seed dispersal (perhaps by toucans). In Cameroon, seed-rain samples from 12 months of trapping (totalling 77.9 m²) below endozoochoric trees contained only one *Erythrina* seed (C. Clark, 2000, unpublished data). The same pattern was found for *P. broteroi* in Sierra de Cazorla, Spain. Three years of data on seed fall (1200 traps) contained only one record of a dispersed seed, 13 m away from the nearest *Paeonia* adult (J.L. Garcia-Castaño and P. Jordano, 2000, unpublished data). Likewise, Foster and Delay (1998) reported that, in 85 h of watching *Ormosia* trees (three species),

only 19 seeds were dispersed away from the trees and only one was swallowed by birds. Peres and van Roosmalen (1996) did not record any arboreal frugivores ingesting *Ormosia lignivalvis* in 185 h of focal tree observations.

However, our findings should not be taken out of the context of the plants' demography. In particular, we measured only the number of seeds dispersed, not seedling establishment. The low frequency of seed dispersal means either low selection or low reproduction. Several additional issues should be pursued to understand the mimetic fruit-dispersal system. Would results have been different if the seeds were black in colour? Would a tree actually have higher fitness if it put a nutritive reward on its seeds? To what extent does the maintenance of scarce populations of mimetic-fruited species depend on rare events of seed dispersal by frugivores?

Although mimetic fruits are extremely difficult to study in the wild, study of their seed-dispersal systems may be as informative as the study of more typical fruits and is paramount for understanding the evolution of plant–frugivore interactions. The balance between fruit attraction and chemical defence may be better understood when both extremes of the deception–reward gradient are considered.

Acknowledgements

I am deeply grateful to all students of the Plant Phenology and Seed Dispersal Research Group, particularly Liliane Zumstein, Inez Morato and Paulo Guimarães, Jr, for their help in the field and aviary experiments and to Ana Tozzi for enlightening discussions on *Leguminosae* phylogeny. I also thank the administration of Bosque dos Jequitibás in Campinas and Mr Roberto Azeredo from CRAX for allowing our trials with their captive birds. I am grateful to Instituto Florestal and Fundação Florestal de São Paulo for providing all facilities at EE Caetetus and Parque Intervales. My thanks also go to C. Clark, J.S. Wright and J.L. Garcia-Castaño for allowing me to use their data on seed fall. Daniel Janzen, Pedro Jordano, Carlos Herrera, Douglas Levey and

Marco A. Pizo provided helpful discussion and helped improve the manuscript. Finally, I thank FAPESP (Fundação de Ampara a Pesquisa do Estado de São Paulo) (96/10464-7) and CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico) (300025/97-1) for financial support.

References

- Aleixo, A. and Galetti, M. (1997) The conservation of the avifauna in a lowland Atlantic forest in southeast Brazil. *Bird Conservation International* 7, 235–261.
- Armstrong, W.P. (1992) Jewels of the tropics. *Terra* 30, 26–33. (<http://waynesword.palomar.edu/ww0901.htm>)
- Barrows, E.M., Acquavella, A.P., Wesinstein, P.J.S. and Nosal, R.E. (1980) Response to novel food in captive, juvenile mockingbirds. *Wilson Bulletin* 92, 399–402.
- Blake, J.G. and Loiselle, B.A. (1992) Fruits in the diets of neotropical migrant birds in Costa Rica. *Biotropica* 24, 200–210.
- Bockerman, W.C.A. (1991) Observações sobre a biologia do macuco *Tinamous solitarius*. PhD thesis, Universidade de São Paulo, Brazil.
- Bruneau, A. (1996) Phylogenetic and biogeographical patterns in *Erythrina* (*Leguminosae: Phaseoleae*) as inferred from morphological and chloroplast DNA characters. *Systematic Botany* 21, 587–605.
- Cipollini, M.L. and Levey, D.J. (1997) Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypothesis and implications for seed dispersal. *American Naturalist* 150, 346–372.
- Corner, E.J.H. (1949) The Durian theory or the origin of the modern tree. *Annals of Botany* 52, 367–414.
- Cowan, R.S. (1998a) *Pararchidendron*. In: Orchard, A. (ed.) *Flora of Australia, Mimosaceae (excl. Acacia), Caesalpinaceae*. CSIRO, Melbourne, Australia, pp. 39–40.
- Cowan, R.S. (1998b) *Archidendron*. In: Orchard, A. (ed.) *Flora of Australia, Mimosaceae (excl. Acacia), Caesalpinaceae*. CSIRO, Melbourne, Australia, pp. 40–48.
- Dafni, A. (1984) Mimicry and deception in pollination. *Annual Review of Ecology and Systematics* 15, 259–278.
- Edmunds, M. (1974) *Defence in Animals*. Longman, Harlow.
- Endler, J.A. (1981) An overview of the relationships between mimicry and crypsis. *Biological Journal of the Linnean Society* 16, 25–31.
- Erard, C., Théry, M. and Sabatier, D. (1991) Régime alimentaire de *Tinamous major* (Tinamidae), *Crax alector* (Cracidae) et *Psophia crepitans* (Psophiidae) en forêt guyanaise. *Gibier Faune Sauvage* 8, 183–210.
- Fischer, K.E. and Chapman, C.A. (1993) Frugivores and fruit syndromes: differences in patterns at the genus and species level. *Oikos* 66, 472–482.
- Foster, M.S. and Delay, L.S. (1998) Dispersal of mimetic seeds of three species of *Ormosia* (*Leguminosae*). *Journal of Tropical Ecology* 14, 389–411.
- French, K. (1990) Evidence for frugivory by birds in montane and lowland forests in southeast Australia. *Emu* 90, 185–189.
- Galetti, M. (1996) Fruits and frugivores in a Brazilian Atlantic forest. PhD thesis, University of Cambridge.
- Galetti, M. and Pizo, M.A. (1996) Fruit-eating birds in a forest fragment in southeastern Brazil. *Ararajuba* 4, 71–79.
- Galetti, M., Martuscelli, P., Olmos, F. and Aleixo, A. (1996) Ecology and conservation of the jacutinga *Pipile jacutinga* in the Atlantic forest of Brazil. *Biological Conservation* 82, 31–39.
- Gamberale, G. and Tullberg, B.S. (1998) Aposematism and gregariousness: the combined effect of group size and coloration on signal repellence. *Proceedings Royal Society of London B* 265, 889–894.
- Gautier-Hion, A., Duplantier, J.M., Quris, R., Feer, F., Sourd, C., Decoux, J.P., Dubost, G., Emmons, L., Erard, C. and Hecketsweiler, P. (1985) Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* 65, 324–337.
- Gould, S.J. and Vrba, E.S. (1982) Exaptation – a missing term in the science of form. *Paleobiology* 8, 4–15.
- Herrera, C.M. (1982) Defense of ripe fruits from pests: its significance in relation to plant–disperser interactions. *American Naturalist* 120, 218–247.
- Herrera, C.M. (1987) Vertebrate-dispersed plants of the Iberian peninsula: a study of fruit characteristics. *Ecological Monographs* 57, 305–331.
- Herrera, C.M. (1992) Interspecific variation in fruit shape: allometry, phylogeny, and adaptation to dispersal agents. *Ecology* 73, 1832–1841.
- Howe, H.F. (1993) Specialized and generalized dispersal systems: where does ‘the paradigm’ stand? *Vegetatio* 107/108, 3–13.
- Howe, H.F. and Smallwood, J. (1982) Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13, 201–228.
- Hurr, K.A., Lockhart, P.J., Heenan, P.B. and Penny, D. (1999) Evidence for the recent

- dispersal of *Sophora* (*Leguminosae*) around the Southern Oceans: molecular data. *Journal of Biogeography* 26, 565–577.
- Janson, C.H. (1983) Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* 219, 187–189.
- Janson, C.H. (1992) Measuring evolutionary constraints: a Markov model for phylogenetic transitions among seed dispersal syndromes. *Evolution* 46, 136–158.
- Janzen, D.H. (1984) Dispersal of small seeds by big herbivores: foliage is the fruit. *American Naturalist* 123, 338–353.
- Jordano, P. (1995) Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant–animal interactions. *American Naturalist* 145, 163–191.
- Lambert, F. (1989) Pigeons as seed predators and dispersers of figs in a Malaysian lowland forest. *Ibis* 131, 521–527.
- Levey, D.J. (1987) Seed size and fruit-handling techniques of avian frugivores. *American Naturalist* 129, 471–485.
- Levey, D.J. and Grajal, A. (1991) Evolutionary implications of fruit-processing limitations by cedar waxwings. *American Naturalist* 138, 171–189.
- Loiselle, B.A. and Blake, J.G. (1990) Diets of understory fruit-eating birds in Costa Rica: seasonality and resource abundance. *Studies in Avian Biology* 13, 91–103.
- Mack, A.L. (2000) Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism? *Journal of Bioscience* 25, 93–97.
- McKey, D. (1975) The ecology of coevolved seed dispersal systems. In: Gilbert, L.E. and Raven, P.H. (eds) *Coevolution of Animals and Plants*. University of Texas Press, Austin, Texas, pp. 159–209.
- Malo, J.E. and Suárez, F. (1998) The dispersal of a dry-fruited shrub by red deer in a Mediterranean ecosystem. *Ecography* 21, 204–211.
- Miura, S., Masatoshi, Y. and Ratnam, L.C. (1997) Who steals the fruits? Monitoring frugivory of mammals in a tropical rain forest. *Malayan Nature Journal* 50, 183–193.
- Murray, D.R. (1986) Seed dispersal by water. In: Murray, D.R. (ed.) *Seed Dispersal*. Academic Press, London, pp. 49–85.
- Murray, K.G., Winnett-Murray, K., Cromie, E.A., Minor, M. and Meyers, E. (1993) The influence of seed packaging and fruit color on feeding preferences of American robins. *Vegetatio* 107/108, 217–226.
- Ortmann, J., Schacht, W.H., Stubbendieck, J. and Brink, D.R. (1998) The ‘foliage is the fruit’ hypothesis: complex adaptations in buffalograss (*Buchloe dactyloides*). *American Midland Naturalist* 140, 252–263.
- Peres, C.A. and van Roosmalen, M.G.M. (1996) Avian dispersal of mimetic seeds of *Ormosia lignivalvis* by terrestrial granivores: deception or mutualism? *Oikos* 75, 249–258.
- Quin, B.R. (1996) Diet and habitat of emus, *Dromaius novaehollandiae*, in the Grampians ranges, southwestern Victoria. *Emu* 96, 114–122.
- Quinn, J.A., Mowrey, D.P., Emanuele, S.M. and Whalley, R.D.B. (1994) The ‘foliage is the fruit’ hypothesis: *Buchloe dactyloides* (Poaceae) and the shortgrass prairie of North America. *American Journal of Botany* 81, 1545–1554.
- Ramos, M.V., Teixeira, C.R., Bomfim, L.R., Madeira, S.V.F. and Moreira, R.A. (1999) The carbohydrate-binding specificity of a highly toxic protein from *Abrus pulchellus* seeds. *Memórias do Instituto Oswaldo Cruz* 94, 185–188.
- Ricker, M., Daly, D.C., Veen, G., Robbins, E.F., Sinta, M., Chota, J., Czygan, F. and Kinghorn, D. (1999) Distribution of quinolizidine alkaloid in nine *Ormosia* species (*Leguminosae-Papilionoideae*). *Brittonia* 51, 34–43.
- Ridley, H.N. (1930) *The Dispersal of Plants Throughout the World*. L. Reeve, London.
- Ritland, D.B. (1991) Revising a classic butterfly mimicry scenario: demonstration of Müllerian mimicry between Florida viceroys (*Limenitis archippus floridensis*) and queens (*Danaus gilippus berenice*). *Evolution* 45, 918–934.
- Rudd, V.E. (1965) The American species of *Ormosia* (*Leguminosae*). *Contributions of United States National Herbarium* 32, 279–284.
- Santamaria, M. and Franco, A.M. (2000) Diet of the curassow *Mitu salvini* and the fate of ingested seeds in Colombian Amazon. *Wilson Bulletin* 112, 473–481.
- Snow, D.W. (1971) Evolutionary aspects of fruit-eating by birds. *Ibis* 113, 194–202.
- Sokal, R.R. and Rohlf, F.J. (1995) *Biometry*. W.H. Freeman, New York.
- Steadman, D. and Freifeld, H.B. (1999) The food habits of Polynesian pigeons and doves: a systematic and biogeographic review. *Ecotropica* 5, 13–33.
- Tokarnia, C.H. and Dobereiner, J. (1997) Cross-immunity by the seeds of *Abrus precatorius* and *Ricinus communis* in cattle. *Pesquisa Veterinária Brasileira* 17, 25–35.
- van der Pijl, L. (1982) *Principles of Dispersal in Higher Plants*, 3rd edn. Springer-Verlag, New York.
- Wheelwright, N.T., Haber, W.A., Murray, K.G. and Guindon, C. (1984) Tropical fruit-eating

-
- birds and their food plants: a survey of a Costa Rican lower montane forest. *Biotropica* 16, 173–192.
- Williamson, G.B. (1982) Plant mimicry: evolutionary constraints. *Biological Journal of the Linnean Society* 18, 49–58.
- Witmer, M.C. (1998) Do seeds hinder digestive processing of fruit pulp? Implications for plant/frugivore mutualisms. *Auk* 115, 319–326.
- Yumoto, T. (1999) Seed dispersal by Salvin's curassow, *Mitu salvini* (Cracidae), in a tropical forest of Colombia: direct measurements of dispersal distance. *Biotropica* 31, 654–660.
- Ziburski, A. (1991) *Dissemination, Keimung und Etablierung einiger Baumarten der Überschwemmungswälder Amazoniens*. 77 Tropische und subtropische Pflanzenwelt. Akademie der Wissenschaften und der Literatur, Mainz.