


Decoding Darwin's puzzle: avian dispersal of mimetic seeds

MARCO A. PIZO ^{1,5} ANTONIO B. A. FONTANELLA,¹ GUILHERME CANASSA,¹ WALTER D. ESPÍNDOLA,² CARLOS O. A. GUSSONI,³ ANDRÉ DE C. GUARALDO⁴ AND TOMÁS A. CARLO²

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¹Department of Zoology, Universidade Estadual Paulista, Rio Claro, São Paulo 13506-900 Brazil.

²Biology Department & Ecology Program, Penn State University, University Park, Pennsylvania 16802 USA.

³Universidade Estadual Paulista Julio de Mesquita Filho, Rua 12-B, 621, Vila Indaiá, Rio Claro, São Paulo 13506-746 Brazil.

⁴Zoology Department, Universidade Federal de Juiz de Fora, Minas Gerais, Juiz de Fora, 36036-900 Brazil.

⁵E-mail: marco.pizo@unesp.br

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One and a half century ago, Charles Darwin declared that the so-called mimetic seeds were a “sore puzzle” to him (letter to J. D. Hooker of 10 December 1866; Darwin Correspondence Project, *available online*).⁶ Today the evolutionary ecology of seeds that in coloration resemble fleshy fruits, but that do not offer food rewards to mutualistic frugivores, is still intriguing. Two hypotheses were proposed to explain the interaction of mimetic seeds with seed dispersers: the *mutualistic hypothesis* suggests that mimetic seeds are dispersed by terrestrial birds that use the hard seeds as grit to mechanically digest food in the gizzard (Peres and Van Roosmalen 1996). According to this hypothesis, seed coloration does not represent mimetism, but a way to aid in their detection by terrestrial birds. The *mimetic hypotheses* state that mimetic seeds are non-mutualistic and deceive frugivores, especially those naïve individuals that have not yet

learned to avoid these deceptive non-rewarding seeds (Galetti 2002).

Galetti (2002) experimented with captive birds and mimetic seeds of the genus *Ormosia* (Fabaceae) and found support for mimetism. Galetti's work highlighted the role of naïve individuals in the dispersal of mimetic seeds in the field. Galetti also predicted that, precisely because they offer no food reward, mimetic seeds should be more likely to be dispersed during periods of low fruit availability for the bird community. The mimetism hypotheses underscore the importance of community contexts and bird individual experiences in driving the dispersal and natural history trait characteristics in species with mimetic dispersal strategies. For example, if mimetic seeds outnumber legitimate (mutualistic) fleshy fruits, birds can rapidly learn to avoid them (Stourmaras et al. 2015). Therefore, the frequency of dispersal of mimetic seeds should be greater when their abundance is lower relative to the abundance of fruits with real nutritive pulp.

Here we examined the relationship between the presence of naïve birds (i.e., young and migratory birds arriving at the study area) and the abundance of fruits, with the dispersal rate of the mimetic seeds of *Rhynchosia melanocarpa* Grear. (Fabaceae), a vine whose pods contain one or two black and red seeds (4.7 mm length × 3.9 mm width) that emulate many bicolored arilated seeds (Fig. 1). We compared the dispersal rate of *R. melanocarpa* with two fleshy-fruited species, *Ocotea pulchella* (Lauraceae; 7.7 × 6.0 mm, one seed per fruit) and *Schefflera vinosa* (Araliaceae; 7.2 × 8.5 mm, two seeds per fruit). We predicted (1) a greater increase in the seed rain of *R. melanocarpa* relative to fleshy-fruited species at the time when naïve birds appear in the community, and (2) a peak in the dispersal of *R. melanocarpa* seeds when its relative availability was lowest relative to fleshy fruits.

The study was conducted in an area of disturbed Cerrado vegetation in Rio Claro, São Paulo, Brazil (22°23'38.65" S, 47°32'25.70" W; 620 m above sea level). The area presents a typical Cerrado physiognomy (Oliveira and Marquis 2002), with trees up to 5 m tall and shrubs, but instead of native herbs, it has a dense layer of the exotic grass *Urochloa* sp. In this area, we established a 1.5-ha plot subdivided in 10 × 10 m cells (Morán-López et al. 2019). A patch of sparse *Eucalyptus* trees (10–15 m tall) occupied the center of the plot. *Copaifera langsdorffii* (Fabaceae), a species with capsule arilated fruits that could serve as models for the mimetic species, is present in the vicinity of the plot.

Once a week, from August 2018 to January 2019, we counted the number of mature bird-dispersed fruits at each plot cell. When a plant had too many fruits to be

⁶ <https://www.darwinproject.ac.uk/letter/DCP-LETT-5300.xml>



FIG. 1. The picture shows opened pods of *Rhynchosia melanocarpa* exposing the black and red mimetic seeds. The inset shows a seed of *R. melanocarpa* among the seeds of fleshy fruits on a seed trap. Photo credit: Ruben Queiroz (plant) and T. Carlo (seed in trap).

counted, we visually estimated the fruit production by counting the number of fruits in selected branches and extrapolated to the entire plant. Concurrently we sampled the seed rain with one hundred seed traps placed beneath trees and shrubs throughout the plot. Each trap measured 0.5×0.5 m and consisted of window screen cloth suspended 15 cm from the ground on a wire frame. Once a month, we collected trap contents and counted the number of seeds. We did not consider the seeds in traps that had a plant of any of the focal species above as these seeds might have simply dropped from the overhanging plant without being actually dispersed by a bird.

From November 2017 to January 2019, we walked the plot at least once a week at morning and afternoon periods to record bird frugivory. Bird abundance was assessed every week with a 5-min point count conducted from a randomly selected grid cell within the plot. Counts were sampled in the morning (06:30–08:00), and only birds seen or heard inside the plot were recorded. The monthly abundance of all frugivorous bird species was expressed as the point count abundance index given by the ratio between the total number of bird records and the total number of points sampled in a given month (Blondel et al. 1970).

To examine the temporal abundance of young birds, we used data from a long-term mist netting study conducted from 2012 to 2018 in an area adjacent to the plot.

In this study, from four to six nets (6–12 m length, 36-mm mesh) were set every 1–3 weeks from 06:00 to 11:00 yielding a sampling effort of $154,423 \text{ h-m}^2$ well distributed over the months. All captured birds were marked with coded aluminum bands. Birds were categorized as young or adult based on plumage characteristics and/or the presence of bill commissures. Recaptures were not considered for analyses. Only bird species detected within the plot were considered in the analyses.

From 2003 to 2019, we made daily search of migratory birds in the period expected for their arrival at the area. We then compiled the month of arrival for the five migratory frugivorous species detected at the plot (Tyrannidae: *Myiodynastes maculatus*, *Tyrannus savanna*, *T. melancholicus*, *Empidonomus varius*; Vireonidae: *Vireo chivi*).

We found a total of 18 dispersed seeds from *R. melanocarpa* (monthly average \pm SE = 3.0 ± 1.0 seeds), 26 *O. pulchella* seeds (4.3 ± 1.8 seeds), and 807 *S. vinosa* seeds (134.5 ± 70.5 seeds) in the seed traps. Fruit production of *R. melanocarpa* and *S. vinosa* peaked in September, while *O. pulchella* peaked in October (Fig. 2A). *Rhynchosia melanocarpa* represented 50% of the fruits in the plot at the fruiting season onset (August–October), and dropped to around 10% toward the end of the fruiting season (Fig. 2A). In the seed rain, the peak of *R. melanocarpa* occurred in August and sharply dropped after, contrasting with *O. pulchella* and *S.*

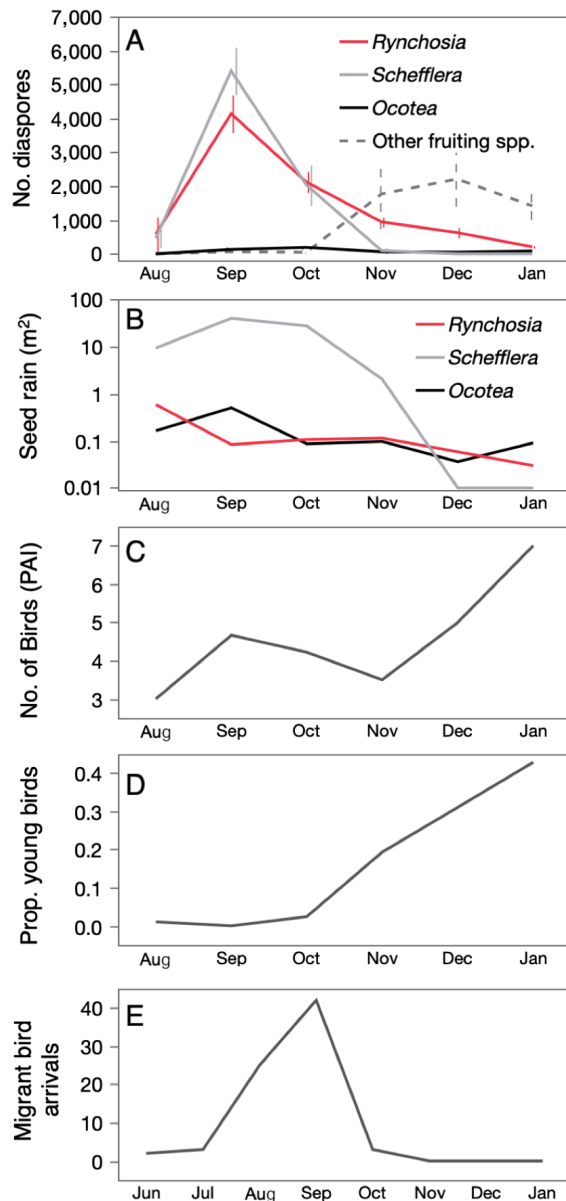


FIG. 2. Monthly values for (A) production of *Rhynchosia melanocarpa* seeds, *Ocotea pulchella* and *Schefflera vinosa* fruits, and all other fleshy bird-dispersed fruits in the study plot (average values are accompanied by vertical lines representing standard errors); (B) density of *R. melanocarpa* seeds sampled in 100 0.25-m² seed traps (note the log scale of the y-axis); (C) the abundance of frugivorous birds in the plot as given by the point count abundance index (PAI); (D) the proportion of young birds in relation to all frugivorous birds captured in mist nets; and (E) the monthly frequency of arrivals of migratory species. The time span for all graphs is August 2018 to January 2019, except (C) that pooled birds captured in mist nets from 2012 to 2019, and (E) that compiled data gathered from 2003 to 2019.

vinosa whose seed rain followed their fruit abundance pattern in the environment (Fig. 2B).

We obtained 732 frugivory records of 30 bird species feeding on the fruits of 19 plant species, but none of the records included *R. melanocarpa* seeds, while *O. pulchella* had 5 and *S. vinosa* had 139 bird frugivory records. The abundance of bird species fluctuated over the fruiting season with no relation to overall fruit abundance ($r^2 = 0.001$, $P = 0.95$; Fig. 2C). There was no coincidence in the dispersal of *R. melanocarpa* or any of the two fleshy-fruited species with the appearance and subsequent increase in the abundance of young birds in the environment (Fig. 2D). Migratory birds arrived mostly between August and September (Fig. 2E).

The dispersal of *R. melanocarpa* peaked at a time when its fruits were just starting to become ripe and when other fleshy fruits also started to become available following the dry season of severe fruit scarcity. Arguably, birds quickly learned to avoid the mimetic seeds and the dispersal of *R. melanocarpa* rapidly dropped despite an increase in fruit availability, whereas the dispersal of *S. vinosa* and *O. pulchella* were positively correlated with their availability in the environment (Fig. 2A, 2). The input of naïve birds could have increased the dispersal of *R. melanocarpa* seeds, but contrary to our expectations, the peak dispersal of *R. melanocarpa* seeds did not coincide with the appearance of young birds in the community but instead coincides with the arrival of migratory birds in the area (Fig. 2E). Most seed dispersal of *R. melanocarpa* occurred when it was quite dominant and not when it was proportionally rare in the community (i.e., compared to fleshy fruits, Fig. 2A). Additionally, the temporal pattern of seed dispersal was uncorrelated to the global abundance of frugivorous birds.

What can explain our observations for the temporal pattern of seed rain of the mimetic seeds of *R. melanocarpa*? In the highly seasonal environment of the Cerrado, fleshy fruits are not produced year-round but in a well-defined fruiting season and thus the first fruits to become available can be avidly disputed by birds. Our results show that the dispersal of mimetic seeds is greatest at the onset of the community fruiting season. This period lies outside of the main breeding season of the bird community, and thus there are no young naïve birds in the area yet, but the arrival of migratory birds may promote the dispersal of *R. melanocarpa* seeds. Following the season of fruit scarcity, it is possible that even experienced birds forget that *R. melanocarpa* is a scam, which raises the question of the role of foraging memory in the choice of the newly available fruits.

It has been documented that previous foraging experiences of birds have long-lasting effects on food selection (Schaefer et al. 2008), and thus, mimetic seeds should be

avoided by experienced individuals. But theory also predicts that past experiences can be downplayed in highly heterogeneous environments (Hirvonen et al. 1999). In fact, the Cerrado is a highly seasonal biome (i.e., temporal heterogeneity) where the availability of fleshy fruits drastically varies with time (Camargo et al. 2013, Morellato et al. 2013). Our results suggest that mimetic seeds benefit from this seasonal heterogeneity by becoming available early in the fruiting season to profit from the “willingness” of birds to eat fruits and there is a greater influx of migratory bird species. Our observations also suggest that birds learn to avoid mimetic seeds as the fruiting season progresses. Still, although seed removal of *R. melanocarpa* decreases sharply after it first appears, it always receives some level of seed dispersal, possibly because of the influx of naïve birds into the community as the nesting season kicks in, the occasional immigration of inexperienced adults into the locality, and the arrival of migratory birds.

In summary, having seeds available and relatively abundant right at the beginning of the fruiting season of a highly seasonal plant community appears more important for dispersal of mimetic seeds than rarity in the community or its reliance on naïve young birds. This particular period happens to coincide with the arrival of many migrant bird species that could be exploited by *R. melanocarpa* since many migratory individuals could be as prone to deception as the young and naïve birds of the local community. This dispersal strategy contrasts with those that will be more effective in a less seasonal environment where dispersal of mimetic seeds may be more evenly distributed throughout the year and benefit more from remaining proportionally rare in the community (Galetti 2002).

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