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SHORT COMMUNICATION

Short-term fruit removal from a neotropical shrub with experimental bicoloured displays

Daniel G. Wenny[1]

Illinois Natural History Survey, 3159 Crim Dr., Savanna, Illinois 61074, USA
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Interest in the colour of fruits eaten by vertebrates has a long history (Ridley 1930, Turcek 1963, van der Pijl 1972). Within a given geographical area, colours of bird-consumed fruits compared with mammal-consumed fruits are fairly consistent (Janson 1983, Wheelwright & Janson 1985, Willson & Whelan 1990), but comparisons among different regions reveal selective pressures of different animal groups (Lord 2002, Willson *et al*. 1989). One consistent pattern among regions is that fruits with a two-colour display typically are eaten by birds (Wheelwright & Janson 1985, Willson & Thompson 1982, Willson & Whelan 1990). Thus, it is thought that such bicoloured displays are specifically adapted to attract birds and plants with these displays presumably benefit from seed dispersal by birds (Janson 1983, Willson & Whelan 1990).

Two general types of bicoloured displays are recognized. Structural or morphological bicoloured displays are typically defined as those in which the fruit, or part of a fruit, is one colour (often blue or black) and an adjacent structure is a contrasting colour (often red). Adjacent contrasting structures include capsules, bracts, stems or pedicels (Wheelwright & Janson 1985, Willson & Thompson 1982). Polychromic species may be considered a type of structural bicoloured display (Lee *et al*. 1988, Willson & O'Dowd 1989), but typically the different colour morphs occur on different individuals (Gervais *et al*. 1999, Traveset & Willson 1998, Traveset *et al*. 2001, Willson 1983). A broad definition of structural bicoloured displays may include deciduous foliage changing colour (Stiles 1982), but this idea has been challenged (Herrera 1982, Willson & Hoppes 1986). Temporal bicoloured displays are those in which ripe fruits contrast with ripening fruits, both of which contrast with the foliage (Willson & Thompson 1982). Fruits of temporal bicoloured displays undergo two colour changes while ripening (often green to red to black), and thereby may provide information about fruit quality (i.e. which fruits are ripe, Greig-Smith 1986, but see Janson 1987).

All bicoloured displays presumably enhance conspicuousness of ripe fruits to birds, which could lead to higher fruit consumption and more seeds dispersed. Although fruit consumption does not always result in effective seed dispersal, without consumption dispersal and recruitment would be greatly reduced (Chapman & Chapman 1995, Cordeiro & Howe 2001). Thus, it is reasonable to assume a general increase in seed dispersal with increased fruit consumption. Experimental manipulations testing the effect of temporal bicoloured displays on removal, however, have yielded mixed results. Such displays generally increased fruit removal for *Prunus serotina* but not for *Rubus occidentalis* (Morden-Moore & Willson 1982, Willson & Melampy 1983). Bicoloured displays in *Pistacia terebinthus* may increase fruit removal but unripe fruits (which do not abscise) may interfere with accessibility of ripe fruits to birds (Fuentes 1995). Evidence for the effect of structural bicoloured displays is also mixed. Artificial bicoloured displays did not increase removal for *Cornus* sp., *Vitis* sp. or *Parthenocissus quinquefolia* (Willson & Hoppes 1986) but did increase removal for *Phytolacca americana* (Whelan & Wilson 1994, Willson & Melampy 1983), *Rhus glabra* (Facelli 1993) and *Lonicera involucrata* (Burns & Dalen 2002). All of these species normally have bicoloured displays except *Rhus*.

To date all experimental studies of bicoloured displays have been conducted in the north temperate zone but bicoloured displays, especially structural ones, are very

[1] Email: dwenny@inhs.uiuc.edu

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common in the tropics (Wheelwright & Janson 1985). In this experiment I manipulated the colour display of a common tropical shrub to test the hypothesis that bicoloured displays enhance fruit removal. This is one of the first tropical studies to test the effect of manipulated colour displays on fruit removal by birds (Altshuler 2001).

Psychotria pittieri Standl. (Rubiaceae), a common understorey shrub in second-growth lowland forests of Costa Rica, occurs in patches of up to several hundred individuals. Each plant produces several infructescences of 10–50 blue two-seeded fruits (approximately 5 mm diameter) that ripen between August and May (Loiselle 1987). Understorey birds such as manakins (Pipridae) and thrushes (*Turdus*) are the main consumers of the fruits and dispersers of the seeds (Denslow & Moermond 1982, Loiselle 1990, Poulin & Lefebvre 1996).

This study was conducted in March 1989 at La Selva Biological Station, Heredia Province, Costa Rica (described in McDade *et al*. 1994). Nine patches of *Psychotria pittieri* were selected in secondary forest and abandoned plantations. Four patches had both experimental and control treatments while five other patches had only controls. Within the first four patches plants were randomly selected and assigned to one of three treatments: (1) artificial bicolour display via addition of a red 'bract'; (2) bract control via addition of a green 'bract'; and (3) control with no bract added. Red bracts were used because red is a common colour of 'bird fruits' and is not visible to most mammals and insects (Wheelwright & Janson 1985, Willson & Whelan 1990). The green bracts were not the exact same shade of green as *Psychotria* leaves to human eyes but they were not as easily visible from a distance as the red bracts were. In addition, *Psychotria pittieri* occurs in relatively open secondary forest with dappled sunlight, so the light environment of *Psychotria* patches is one of varying shades of green. It was not possible to measure the reflectance of the experimental bracts and although avian vision differs from that of humans (Bennett *et al*. 1994), the two control treatments allow a test of the effects of the artificial bracts independent of the colour.

Experimental bracts were 90-mm-diameter circles of coloured cardboard. A slit and central hole allowed the bract to be placed around the stem and supported by the pair of leaves below the infructescence. In each experimental patch, 10 plants had a red bract added, 10 plants had a green bract added and five plants had no bract. In each of the remaining five patches, five plants were randomly selected for the no-bract treatment. At the beginning of the experiment fruits were removed from each plant so that each had only one infructescence with 10 fruits. The ground below each plant was cleared of leaf litter and fallen fruits so that fruit fall could be quantified.

Fruits were monitored daily for 7 d. At each census fruits not present were classified as either dropped, partially eaten or removed. Intact fruits found in the cleared area directly below each plant were considered dropped as a result of natural abscission. Partially eaten fruits were attributed to ants. Ants were occasionally seen on the fruits and removed pieces of the pulp over 2–3 d, often leaving the seeds still attached to the plant. Removed fruits were those not accounted for by the dropped and partially eaten fruits. Removed fruits were assumed to be taken by birds (Altshuler 2001, Denslow & Moermond 1982, Loiselle 1990).

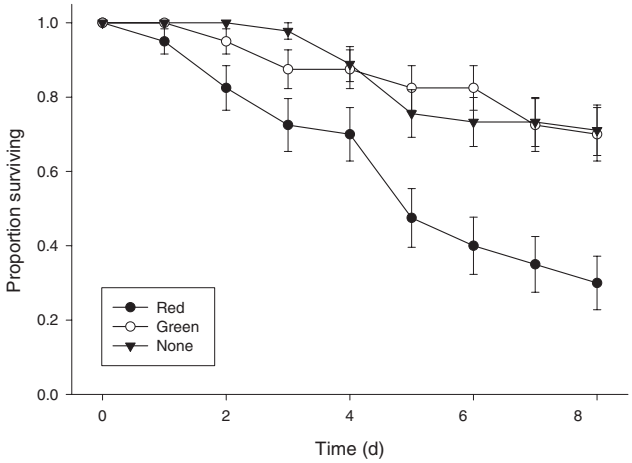


Figure 1. Failure rates of infructescences with red, green or no bract added based on the Kaplan–Meier survival function. The failure time of an infructescence was defined as removal of the first fruit regardless of the total number removed. Rates differed significantly among the three treatments (Mantel log-rank test $\chi^2 = 21.6$, df = 2, $P < 0.001$).

Data were analysed with Systat 8.0 (SPSS 1998). Fruit removal rate was compared among the three treatments with survival analysis and the Mantel log-rank test. The Mantel test weighs each failure interval equally and is appropriate because fruit removal was fairly constant over the course of the study (Figure 1). An infructescence was considered to have survived until the first fruit was removed, and thus removal of one fruit constituted failure.

Differences among treatments in mean removal per plant, visits per plant and removal per visit were analysed with Kruskal–Wallis one-way ANOVA tests. A visit was defined as the removal of at least one fruit between census periods. Because multiple removal events from a given infructescence may not be independent, I also did Pearson chi-squared tests on the number of plants in each treatment that had at least one fruit removed. The survival and chi-squared analyses also were done for dropped and partially eaten fruits.

Fruits from infructescences with red bracts were removed significantly faster than those from infructescences with green bracts (Mantel log-rank test $\chi^2 = 13.3$, df = 1, $P < 0.001$; Figure 1) or no bracts (Mantel $\chi^2 = 14.7$, df = 1, $P < 0.001$). Fruit removal rate did not differ between green and no bracts (Mantel $\chi^2 = 0.01$, df = 1, $P = 0.9$). Failure rates due to fruit drop (Mantel $\chi^2 = 1.9$, df = 2, $P = 0.37$)

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Table 1. Loss of fruits attributable to removal by birds (fruit removal), natural abscission (fruits dropped), and insects (insect damage) among infructescences with red, green or no bract added. Pearson χ^2 test statistics (df = 2) and associated P values are listed in the last row.

	Number of infructescences with		
Treatment (N)	Fruit removal	Fruits dropped	Insect damage
Red (40)	28	26	8
Green (40)	12	26	9
Control (45)	13	27	11
Pearson χ^2 (P)	18.4 (< 0.001)	0.3 (0.8)	0.2 (0.9)

or to fruits eaten by insects (Mantel $\chi^2 = 0.18$, df = 2, P = 0.92) did not differ among the three treatments.

The proportion of infructescences with at least one fruit removed differed significantly among the treatments with red having more than twice the number with removal than either green or controls (Table 1). The proportions of infructescences with natural fruit drop and insect damage were similar among the treatments (Table 1). The average number of fruits removed per infructescence, number of visits per infructescence, and number of fruits removed per visit were all significantly greater for the red treatment than for either the green or control treatments (Table 2).

The addition of red bracts to infructescences increased fruit removal by every measure. Not only did the red bract treatment receive more visits than green or no-bract treatments, but the number of fruits removed per visit was greater, the removal rate was faster, and the total number removed was greater. These results suggest that bicoloured displays are an advantage over monochrome displays in terms of the number of seeds removed from the plant by potential avian seed dispersers.

The equivocal support for the effect of bicoloured displays on removal in previous studies may be a result of several factors. First, with one exception (Facelli 1993) all previous studies were conducted on species that normally have bicoloured displays, and the context of the fruit display was not altered radically in most studies. For two studies in which the colour display was novel, as opposed to a manipulation of an existing display, the effects on fruit removal of artificial red bracts were fairly strong (Facelli 1993, the current study). In contrast, Willson & Hoppes (1986) found no effect of novel colour displays (artificial leaves) on fruit removal but because sample sizes were small (3–5 infructescences per treatment), their results are not strong evidence against the enhancement effect of bicoloured displays.

Second, most previous work on the effects of bicoloured displays has been done in North America where fleshy-fruited species mainly produce fruit in the autumn (August–October) and are eaten by migratory passerine birds. Particularly for temporal bicoloured displays, it is thought that fruit availability corresponds with a period of low abundance and diversity of avian frugivores (Willson & Thompson 1982). Fruit removal in these studies was often highly variable and subject to the vagaries of avian migration. For the present study (conducted in early March), most birds in the area were residents even including Nearctic–neotropical migrants that would have been in the area for 5–7 mo. Thus, this study probably was not confounded by either low frugivore abundance or by a major migration period.

Third, most experiments take place over a short portion of the total fruiting period. Most studies note great variability in fruit removal. It could be that the selective advantages of bicoloured displays are temporally variable during the fruiting season and the timing of an experiment may or may not coincide with a period in which the tested effect is actually important (Herrera 1986, Howe 1984). This variability may contribute to the lack of support in some specific studies for the benefit of bicoloured displays. Longer-term studies as well as efforts to link fruit removal with seed dispersal and seedling establishment (Gervais *et al*. 1999, Herrera *et al*. 1994, Traveset *et al*. 2001) are necessary to firmly establish this connection.

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Table 2. Summary of fruit removal and visit data for 10-fruit infructescences of *Psychotria pittieri* with red bract added, green bract added or no bract. A visit (presumably by birds) is defined as removal of at least one fruit between census periods. Values are mean ± 1 SD. Kruskal–Wallis test statistics for nonparametric one-way ANOVA (df = 2) and associated P values are listed in the last row.

Treatment (N)	Fruits removed per infructescence	Visits per infructescence	Fruits removed per visit
Red (40)	2.0 ± 2.3	0.9 ± 0.9	2.2 ± 1.5
Green (40)	0.7 ± 1.2	0.4 ± 0.6	1.8 ± 1.1
Control (45)	0.6 ± 1.4	0.4 ± 0.6	1.6 ± 1.9
Kruskal–Wallis (P)	21.4 (< 0.001)	14.2 (0.001)	6.6 (0.03)

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