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Experimental evaluation of the foliar flag hypothesis using fruits of *Rhus glabra* (L.)

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Abstract. I tested experimentally whether the presence of colorful plastic ovals (simulating foliar "flags") attached to infructescences of *Rhus glabra* increase fruit removal by birds in a forest-oldfield border. I used a factorial experimental design testing for the effect of size (small or large) and color (yellow or red) of the flags. There was also a control, without flags. Large red flags increased the percent of fruits removed from the panicles, but yellow and small flags had no effect. My results give partial support to Stiles (1982) hypothesis that early color change of leaves close to the fruits in some plants may serve as visual signals that attract frugivorous birds and enhances seed dispersal.

Key words: Frugivorous birds – Plant-animal coadaptations – Temperate North America – Seed dispersal

Interactions with animals may be a prime factor affecting plant evolution, and eventually leading to coadaptations (e.g., Mosquin 1971; Benson 1975; Rhoades 1979; Futuyma and Slatkin 1983). The extent and degree of coevolution between plants and animals has been disputed (e.g., Strong et al. 1984), in part because direct experimental testing of the adaptive origin of a trait is not feasible.

Many fruits present colorful pericarps or bracts that attract seed dispersers (Stiles 1982; Wheelwright and Janson 1985; Greig-Smith 1986; Janson 1987). Stiles (1982) proposed that some plants in the deciduous forest of eastern North America produce visual signals (foliar flags) to attract frugivorous birds by changing, early in the fall, the color of their leaves. In the only test of this hypothesis to the present, the manipulation of the presence of foliar flags on fruit-bearing branches of *Cornus racemosa/drummondii, Parthenocissus quinquefolia* and *Vitis* sp. had no effect on rates of fruit removal (Willson and Hoppes 1986).

Here I report an experiment designed to test whether the presence of colorful objects (plastic ovals simulating foliar flags) enhances the rate of removal of fruits of *Rhus glabra* L. (smooth sumac, Anacardiaceae). I also tested the effect of color and size of the flags. Contrast of coloration between the fruits and the foliar flags is expected to increase fruit removal (Stiles 1982, but see Willson and Hoppes 1986), and larger flags should be perceived from a greater distance, also increasing bird visitation.

Methods

The species

Rhus glabra is a shrub common in roadsides, waste sites, and oldfields in eastern North America. It produces compact panicles with dark red fruits early in the fall. The fruits are dispersed by birds, but they are neither very nutritious nor preferred by birds (Stiles 1980, but see Martin et al. 1951 on the importance of sumacs as a winter food source for wildlife). The seeds are covered by a hard testa; germination is greatly enhanced by soaking the seeds in concentrated sulfuric acid (Brinkam 1974). This suggests that fruit consumption by birds may be essential to secure germination. Late in the summer or early in the fall, the upper leaves of the ramets turn red, acting as a signal to attract migrating birds according to Stiles' (1982) hypothesis. Stiles also assumed that the change of color of the upper leaves must result in a substantial reduction of photosynthesis. This loss of photosynthesis should at least be compensated by the fitness gain produced by enhanced dispersal (Stiles 1982).

Experimental setting

The experiment was conducted at The William L. Hutcheson Memorial Forest Center, Millstone Township, New Jersey. The Center is a mosaic of oldgrowth mixed oak forest, disturbed woodlots, and different-aged oldfields, which attracts a variety of migrating birds. The experiment was begun on 24 October 1988, in the

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border between a young oldfield and a woodlot, a typical habitat for *R. glabra*. No frost had occurred at the time, and the upper and middle leaves of *R. glabra* presented a dark red color, while the basal leaves were still green. Birds, particularly wood thrushes, were abundant and very active in the area at the time. The experiment was a complete factorial, with color and size as factors, each factor combination replicated four times. Sixteen panicles of *R. glabra*, containing around 230 fruits each, were fixed to the end of 1.5 m long wooden sticks, with artificial plastic flags attached 10 cm below the insertion of the panicle, and at a 45° from the horizontal. I used plastic, rigid, oval flags of two different sizes (12 × 8 cm, small flags, and 18 × 12 cm, large flags) and colors (red and yellow). To control for the presence of the flags, eight panicles were attached to sticks without flags. The experimental units were evenly spaced in random order along a 72 m long row along the edge between a woodlot and a 2-year-old oldfield.

Due to the structure of the panicles of *R. glabra*, it was impossible to count the exact initial number of fruits per panicle. Before setting the experiment, 14 panicles, taken at random from a total of 38 similar-sized panicles, were weighed and the total number of fruits counted. Since there was a highly significant correlation ($r = 0.8451$, $P < 0.01$) between weight of the panicle and number of fruits, I weighed the panicles to be used in the experiment, and used the linear regression between weight of panicle and number of fruits to estimate the initial number of fruits.

On 19 November the panicles were retrieved from the field and the remaining fruits counted. I calculated the proportion of fruits removed, and applied a two-way ANOVA to the arc sin-transformed data (to increase normality). To detect differences in treatment effects, pairwise comparison by least significant differences (LSD) were performed between each treatment and the control. Previously, to account for the error induced by the initial estimation of the number of seeds, I set a confidence limit ($P < 0.05$) for the regression calculated between panicle weight and fruit number. To be conservative in the rejection of the null hypothesis (no effect of the flags on fruit removal rate) I performed each pairwise comparison using the estimated removal calculated with lower confidence limit for the treatment with higher removal in the comparison, and the upper limit value for the treatment with the lower removal (always the control).

Results and discussion

The effect of color, size, and the interaction of color × size were significant (ANOVA, $P < 0.01$). Large red flags was the only treatment that increased the percent of fruits removed from the panicles over the control (LSD, $P < 0.05$, Fig. 1). The different effects of yellow and red flags indicates that the results cannot be attributed solely to increased shaking of the infructescence by wind, a possible artifact of the experimental design.

My results suggest that colored flags may actually attract birds and promote seed removal, and contrast with those by Willson and Hoppes (1986). The results do not support the prediction that color contrast between the fruits and the foliar flags should increase visitation by birds (Stiles 1982, see also Willson and Hoppes 1986). Indeed, the increase in fruit removal by the red flags could be attributed to an increase in the expected reward of the visit, i.e. the birds may have perceived the flag as a larger concentration of fruits, an effect that could also be produced by the natural foliar flags. The yellow flags contrasted more with the dark red fruits of *R. glabra* than the red flags, but the red flags contrasted more intensely against the green-yellow background produced by the natural vegetation at that time. It is thus also possible that increased fruit removal was due to the contrast of the flags against the color background.

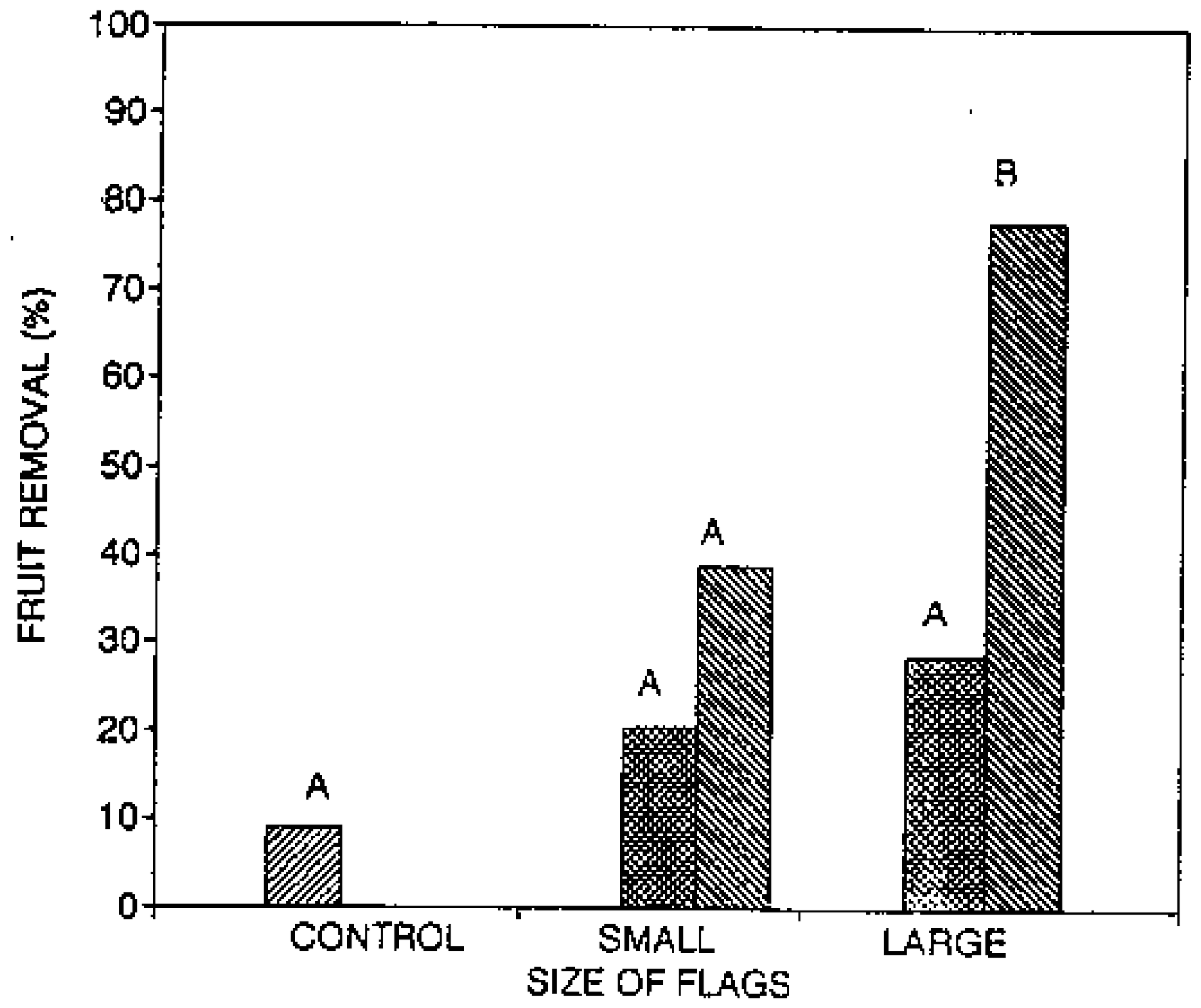

Fig. 1. Percent of fruit of *Rhus glabra* removed from panicles attached to plastic, artificial, foliar flags of two colors (red, *shaded* and yellow, *crosshatched*) and two sizes (small: 12 cm × 8 cm; large 2: 18 cm × 12 cm), or no flag (control). Same *letter* indicates that treatment means are not significantly different from the control after correction using confidence limits (see text for further explanation)

To interpret this evidence as a corroboration of the foliar flag hypothesis requires several assumptions, most conspicuously, that earlier dispersal provides an increase in fitness large enough to compensate for the presumed photosynthetic losses. Furthermore, the cost of changing color early in the fall has not yet been assesed. Nevertheless, this study shows support for the basic tenet of the foliar flag hypothesis. Clearly, experiments capable of distinguishing between the various possible mechanisms mentioned above must be performed to reach more robust conclusions about this hypothesis. This study illustrates how simple field experiments can (and should) be used to test non-trivial predictions made by adaptationist interpretations before accepting its soundness.

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