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THE EFFECTS OF POKEWEED DISPLAY CHARACTERISTICS AND FRUGIVORE IDENTITY ON FRUIT REMOVAL

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ABSTRACT

THE EFFECTS OF POKEWEED DISPLAY CHARACTERISTICS ON FRUGIVORE IDENTITY AND FRUIT REMOVAL

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Fruit color and contrast are important display traits that influence frugivory and seed dispersal. Asynchronous ripening and the presences of unripe fruits in mixed displays can also influence frugivory and seed dispersal. We tested for effects of ripening synchrony in pokeweed (*Phytolacca americana*) by studying fruit removal on plants with varying levels of synchrony. Over the course of our experiment, there was a strong, but non-significant trend for bushes with both ripe and unripe fruits to receive more fruit removal than bushes that were fully ripe. There was also a trend for frugivory to be positively correlated with the proportion of ripe fruit on the bush during the middle and end of the fall fruiting season, but not the beginning. We hypothesize that the presence of unripe fruits on a bush signal the freshness of the fruits that are ripe, and that birds prefer to forage on bushes with freshly ripe fruits. However, the presence of unripe fruits could decrease foraging efficiency, making plants with a large proportion of ripe fruits more attractive to frugivores than plants with a smaller proportion of ripe fruit. In addition to the expected avian frugivory, our pokeweed plants also experienced a great deal of white-tailed deer frugivory, leading to questions about the role deer play in seed dispersal and plant reproduction for pokeweed.

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Introduction

Frugivory is one of the most common and obvious types of mutualistic relationships. While a great deal of work has been done on the interactions between plants that produce fleshy fruits and birds that eat them and disperse their seeds (Snow, 1971; Stiles, 1980; Gosper et al., 2005), it is still not entirely clear how plants attract avian dispersers or to what extent a fruiting plant's seed dispersal might be helped or hindered by attracting other, non-avian, fruit-eaters.

Recent work has demonstrated that both color and the amount of contrast between a fruit and its background may have a significant impact on fruit choice by birds (Willson & Whelan, 1989; Galetti et al., 2003; Schmidt et al., 2004). These results suggest that selection has acted on fruiting displays to attract avian frugivores, rather than to attract other taxa such as mammals or to repel certain destructive taxa of insects. If this is true, we might expect that some of the common visual characteristics of fruiting displays could be explained by avian fruit choice.

The most basic example of a fruiting display is a ripe fruit presented against a background of leaves. However, there are many species that have more complicated displays than this. Fruiting displays with an additional colored component are often referred to as bicolored displays. We avoid the term bicolored display because it implies that two colors are involved in the display, when in fact there are three or more colors present: that of the leaves, the ripe fruit, and an additional colored component. For instance, plants can have temporally mixed displays, in which ripe and unripe fruits are present simultaneously. Other plants have structurally mixed displays; these involve an additional colored component of the plant besides the leaves and fruits. Structurally mixed displays often involve colored stems. Some plants exhibit both structurally and temporally mixed displays at the same time. Mixed displays are fairly common; one study estimated that approximately one-third of the fruiting trees, shrubs, and bushes in Illinois produce them; although only 10% of the fruiting herbs were categorized as mixed displays (Willson & Thompson, 1982).

Many plants exhibit temporally mixed displays due to asynchronous ripening. It could be argued that these mixed displays are a result of physiological constraints preventing synchronous ripening. It is a necessity for many black fruits to change from green to red and finally to black as their anthocyanin concentration increases. However, there are species of plants in which the fruits mature from green to black without transitioning through a red stage (Willson & Thompson, 1982), suggesting that red coloration is not always a necessary physiological precursor to black coloration. In addition, the degree of ripening asynchrony varies greatly between species, and for some plants the asynchrony is negligible (Gorchov, 1990). While these facts do not completely rule out physiological constraints as an explanation for asynchronous ripening for some plant species, they do indicate that such constraints are not entirely limiting. Furthermore, it is possible that avian frugivory could select for temporally mixed displays, increasing asynchrony beyond any that might result from physiological constraints.

A potential explanation for the prevalence of temporally mixed displays among black-fruiting plants is that black fruits accumulate more insect damage than do red fruits (Mordenmoore & Willson, 1982). This might select for the plant to maintain only a few ripe black fruits at any given time. This would decrease the attraction of the plant to insects and restrict the amount of damage that insects can cause within a short timeframe. Neither of these possible explanations addresses the prevalence of structurally mixed displays.

An explanation that could encompass both temporally and structurally mixed displays is the possibility that mixed displays act as either a signal or a cue to attract fruit-eating birds. Schaefer et al. (2007) have shown that, to the avian visual system, the reflectance spectra of secondary components of fruiting displays (unripe fruit, colored bracts, etc.) contrast more against the background leaves than do those of ripe fruit. This suggests that mixed displays render a fruiting plant more visible to frugivorous birds than would otherwise be so.

Many field experiments have investigated the effect of mixed displays on avian fruit choice, but the results have been inconsistent. Several studies compared displays of only ripe fruit to displays of ripe fruit plus an additional color and found that frugivory was higher on the more complicated displays; however the absence of leaves in these experiments makes it difficult to extend the results to most situations in which fruits are grown against a leafy background (Mordenmoore & Willson, 1982; Whelan & Willson, 1994; Burns & Dalen, 2002). Two studies experimented by adding colored material to fully ripe displays, and in both cases the frugivory results varied with the type of color that was added (Facelli, 1993; Cramer et al., 2003). Fuentes (1995) found either increased or decreased frugivory depending on the manner in which the mixed displays were presented. Wenny (2003) found increased frugivory with the addition of mixed displays in the form of colored bracts to small shrubs, but Mordenmoore & Willson (1982) found decreased frugivory on the temporally mixed displays of whole trees. In general, there is some limited evidence that mixed displays increase frugivory, but a more rigorous exploration of the topic is needed to confirm this, as well as to determine why birds might forage more on plants with mixed displays.

Here, we discuss the results of two experiments designed to explore the effects of mixed displays on frugivory. To test for an effect of temporally mixed displays we paired artifically manipulated fully ripe and partially ripe bushes of pokeweed (*Phytolacca americana*) and recorded fruit removal. For this experiment, there are two hypotheses. The first hypothesis is that birds will preferentially forage on plants with higher proportions of ripe fruits; this could lead to more efficient foraging. If this hypothesis is correct, we would predict that fruit removal would be higher on our fully ripe plants than on our mixed bushes containing both ripe and unripe fruits. The second hypothesis is that birds will forage more on bushes containing both ripe and unripe fruits. This could be due to the presence of unripe fruit signaling the freshness and quality of the ripe fruit on the same plant, or it could be a result of unripe fruit adding to the visual display of the plant and rendering it more conspicuous to avian dispersers. If this hypothesis is correct, we would expect to find higher fruit removal on our mixed display bushes than on our fully ripe bushes.

To examine the role of structurally mixed displays, we recorded fruit removal on artificial stems of two different colors that had been placed on pokeweed bushes. Here we hypothesize that the additional contrast presented by reddish-purple stems will attract more birds than the contrast presented by green stems. If this is correct, we predict that stems that we have colored reddish-purple will have more fruits removed than stems that we have colored green.

Materials & Methods

We conducted this study in September through November of 2007 at the Lux Arbor Reserve, part of Michigan State University's Kellogg Biological Station, in southwestern Michigan. The reserve consists of a mixture of secondary forest, wetland, and agricultural habitats. It is home to a variety of frugivorous bird species, including gray catbirds (*Dumetella carolinensis*), American robins (*Turdus migratorius*), and cedar waxwings (*Bombycilla cedrorum*). Lux Arbor also has a large population of white-tailed deer (*Odocoileus virginianus*). All experiments were done with the American pokeweed (*Phytolacca americana*), a native herbaceous plant that produces fleshy fruits that are known to be eaten by birds (Smith & Riley, 1990). Pokeweed plants have bright reddish-purple stems. The unripe green fruits turn reddish-purple when maturing and become black when fully ripe. The fruit may remain green for several months, but once they begin to turn reddish-purple, they become fully black in a few days. Pokeweed seeds do not require gut passage in order to germinate, (Armesto et al., 1983), but seeds that pass through an avian gut are more likely to germinate and have faster germination rates (Orrock, 2005).

Experiment 1

In our first experiment, we investigated the impact of temporally mixed displays on fruit removal. We experimentally manipulated bushes with both ripe and unripe fruits to create pairs of bushes with one fully ripe and one partially ripe bush (n = 22 pairs). To create a bush with only ripe fruits, we randomly selected one bush within the pair and cut off all its fruits that were not fully ripe. We pruned our mixed displays to ensure they contained only racemes with both ripe and unripe fruits. We also equalized the number of racemes within each pair to control for the size of the display. The fully ripe bush and the partially ripe bush within each pair were between 2 and 8m apart. Pairs of bushes were located throughout our field site, and pairs were not placed within 20m of each other. We marked three to five individual racemes on each bush and recorded the number of unripe, ripe, and past ripe fruits on each raceme every other day. Unripe fruits were those that were either green or reddish-purple. Fruits were called ripe when they were fully black. Past ripe fruits were shriveled and desiccated. We also categorized the removal as bird or deer frugivory. Avian frugivory was characterized by the removal of individual fruits while leaving the stem intact. We labeled removal as deer frugivory when all or part of the stem, along with the fruits, had been removed. In addition to the evidence on the stems, many of our instances of deer frugivory were also accompanied by deer prints and scat under and around the bushes, and we often observed deer among our pokeweeds, thus strengthening our interpretation that deer were responsible for this type of fruit removal. We collected data for a total of 72 days; however, in many cases the entire pokeweed clump collapsed or the individual racemes were completely stripped of fruits prior to the completion of our study.

We conducted a census of fruits every other day and calculated fruit removal for each census. We summed the fruit removal for the entire study to determine total fruit removal. Fruit removal for each census *i* was calculated as:

$$\text{Removal}_i = (G_{i-1} + P_{i-1} + B_{i-1}) - (G_i + P_i + B_i) - O + N$$

With $O = (O_i - O_{i-1})$ if $O_i > O_{i-1}$ and 0 if $O_i \leq O_{i-1}$

And $N = G_i - G_{i-1}$ if $G_i > G_{i-1}$ and 0 if $G_i \leq G_{i-1}$

G represents the number of green fruits, P represents the number of purple fruits, B represents the number of black fruits, and O indicates the number of fruits that are past ripe.

To test for variables with significant effects on fruit removal, we used the package nlme in R (Pinheiro et al., 2006; R Development Core Team, 2006) to create a linear mixed effects model for our data with total fruit removal as the dependent variable. We tested for the effects of display treatment, frugivory type, number of fruits on the raceme at the beginning of the study, and the total number of days data were collected (trial duration) by including them as fixed effects in our model. We included pair and bush nested within pair as random effects to account for our paired design. Due to concern about the high degree of correlation between the display treatment and fruit count variables, which could lead to issues of multicollinearity and potentially mask the significance of display treatment, we also ran the model without fruit count. Additionally, we tested for the presence of interactions between our terms; however, no interactions were significant, so we did not include them in our final model. Analysis with the package lme4 yielded similar results, so we do not report them here.

Experiment 2

To examine the effect of structurally mixed displays on fruit removal, we attached artificial stems of two different colors to pokeweed bushes (n = 24 sites) and compared fruit removal on the two types of stems. Each bush received three wire stems painted reddish-purple to match the natural color of the pokeweed stem, and three wire stems painted green to match the color of pokeweed leaves and immature stems. We used an Ocean Optics USB4000 spectrometer to match the color of our artificial stems to the natural color of pokeweed stems and leaves. On each stem, we placed 20 freshly picked pokeweed fruits. Every other day we recorded the number of fruits remaining on the stem and replaced them with fresh fruits. While we cannot say conclusively that missing fruits were removed during frugivory, we did have a number of stems that did not lose any fruits, suggesting they were unlikely to simply fall off. Prior to the peak of the frugivory season, we also conducted a small pilot study in which we left the fruits on the artificial stems for 4 days; during that time we recorded no loss of fruit. This suggests that the fruit loss we recorded was due to fruits being removed from the artificial stems rather than merely falling to the ground. We left the stems on the plants for a total of 15 days; however, some trials were shortened when the pokeweed collapsed or was pushed to the ground.

We conducted three sets of trials throughout the course of our study. As a result, each pokeweed bush had between one and three trials, depending on how long the bush remained standing and retained fruits. This resulted in a total of 61 trials.

We analyzed our data using a linear mixed effects model in R. Using total fruit removal per artificial stem as our dependent variable, we tested the fixed effects of our stem color treatment, the trial identity (1-3, indicative of the time in the season that we conducted each trial), the trial duration (3-15 days), a ripeness index that we calculated as the proportion of racemes on a bush bearing unripe fruit, and the interaction between the ripeness index and the trial identity. We also included bush and individual stem nested within bush as random effects.

Results

Experiment 1

Due to our experimental manipulation, racemes on fully ripe bushes held an average of 47 fruits (46.87 ± 12.47). This was significantly fewer fruits than racemes on our mixed bushes, which had an average of 53 fruits (53.29 ± 11.87; $t = 2.49$, $df = 102$, $p < 0.02$), of which approximately 30 (29.68 ± 16.03) were ripe. The number of fruits on a raceme had a significant positive effect on the total fruit removal on that raceme ($t = 9.032$, $df = 99$, $p < 0.0001$; Table 1). Over the course of the study, racemes on fully ripe bushes lost an average of 42 fruits (41.60 ± 18.74), or approximately 89% of their initial complement of fruits. On bushes with mixed displays, racemes lost an average of 52 fruits (52.46 ± 18.83), which amounted to around 98% of their fruits. This difference in total fruit removal between display treatments was not significant; although there was a very strong trend for mixed displays to have higher removal than fully ripe displays ($t = 1.857$, $df = 99$, $p<0.07$; Table 1). Racemes on fully ripe bushes lost an average of 2.66 fruits (± 8.78) every two days, while racemes on mixed bushes lost an average of 3.033 (± 9.57) every two days.

When we ran ran our model without including fruit count, the effect of display treatment became significant ($t = 3.262$, $df = 100$, $p < 0.002$). The correlation coefficient of 0.765 for fruit count and display treatment suggests the possibility that the two variables might be confounded in our full model. If this is the case, the true effect of display treatment could be closer to what the simpler model reveals. This strengthens the potential for display treatment to have a significant effect on total fruit removal.

The type of frugivory also had a significant effect on fruit removal. Throughout the course of our study, we recorded 840 instances of fruit removal. Of these only 42, or around 5%, were categorized as deer removal. Despite this, deer frugivory was responsible for 26% of the total fruit removal, indicating that individual instances of deer frugivory removed more fruit than did instances of avian frugivory. Indeed, our analysis of total removal per raceme revealed that deer frugivory resulted in significantly larger amounts of fruit removal than avian frugivory ($t = 3.04$, $df = 99$, $p < 0.005$; Table 1). The average total number of berries removed from a raceme that experienced deer frugivory was 53 (52.73 ± 12.77), compared to 44 (44.46 ± 21.14) for racemes experiencing only avian frugivory (Figure 2). Total removal was not significantly correlated with the number of days that removal was recorded ($t = 0.76$, $df = 99$, $p < 0.5$; Table 1).

Table 1. Fixed effects for a linear mixed model predicting total fruit removal per raceme. Model: total fruit removal ~ display treatment + frugivory type + fruit count + trial duration, random effects of pair + pair/bush.

fixed effect	value	std. error	df	t-value	p-value
Intercept	-6.423	5.482	99	-1.172	0.244
Display trt (mixed)	5.138	2.768	99	1.857	0.066
frugivory type (deer)	7.991	2.629	99	3.040	0.003
fruit count	0.932	0.103	99	9.032	<0.0001
trial duration	0.057	0.079	99	0.755	0.452

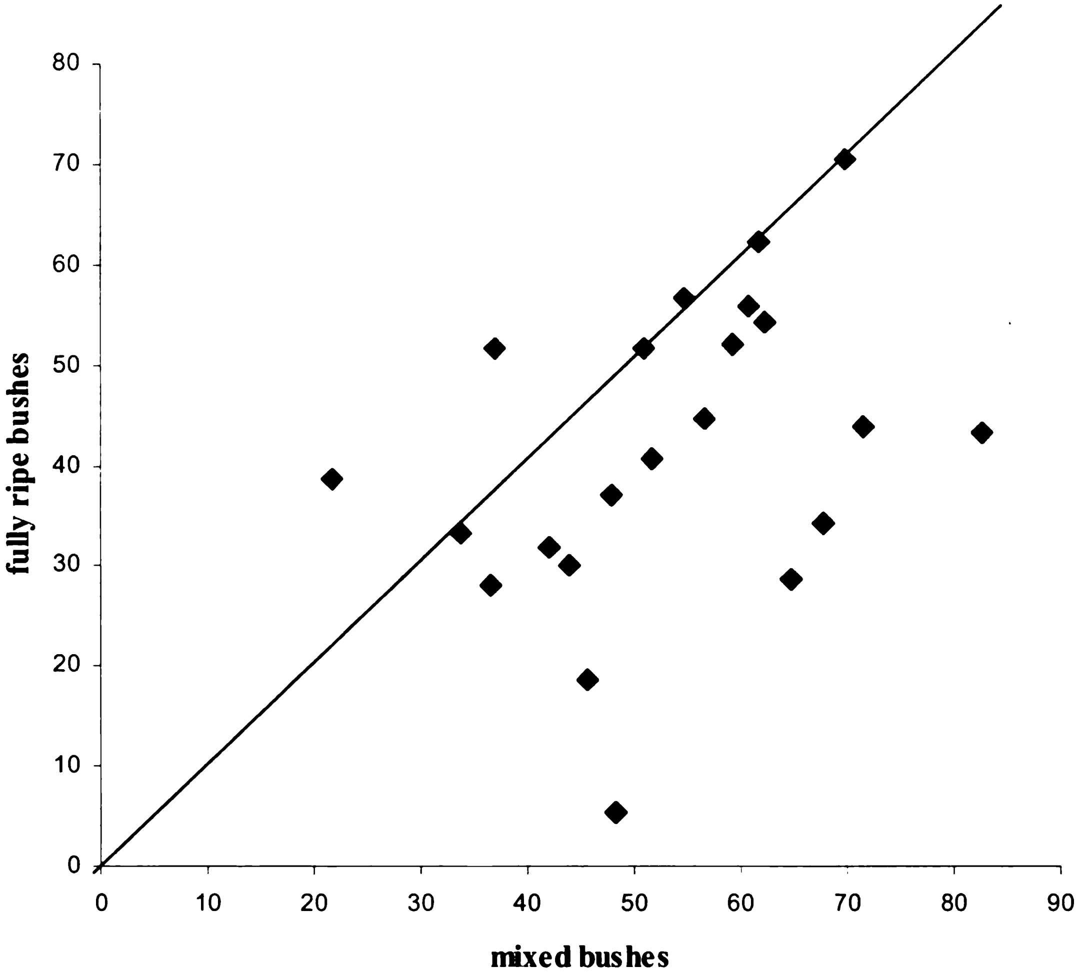

Figure 1. Difference in total removal between mixed and fully ripe treatments at each site. Data points below the line had higher fruit removal on mixed bushes. Data points above the line had higher fruit removal on fully ripe bushes.

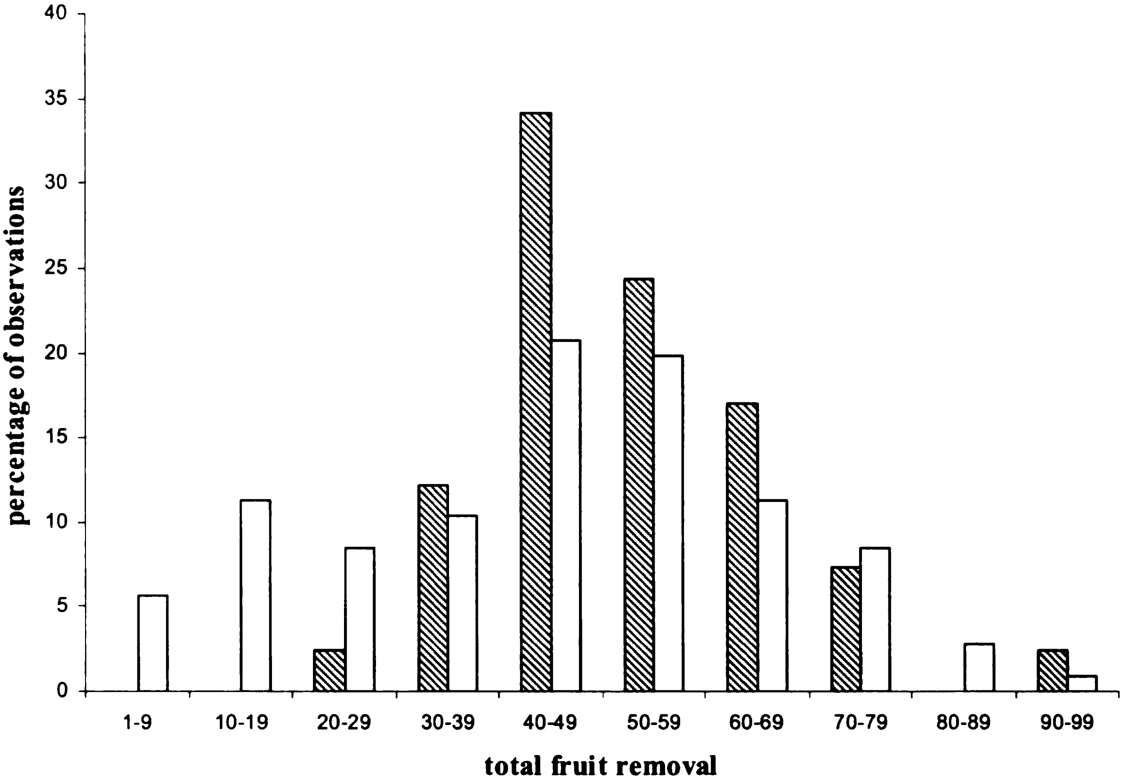

Figure 2. Total number of fruits removed for racemes with and without deer frugivory. Clear bars represent racemes with only bird frugivory. Hatched bars represent racemes that had deer frugivory.

Experiment 2

In our second experiment, we saw considerable fruit removal on both our red and green artificial stems, with each plants' green stems experiencing an average loss of 2 fruits (2.00 ±1.60) every 2 days, and red stems experiencing an average loss of 2.1 fruits (2.10 ± 1.72) every 2 days. However, we found no significant treatment effect ($F = 0.56$, $df = 1,23$, $p > 0.4$). The trial duration, or total number of days the stems were on the bush, was not significantly related to total removal ($F = 0.471$, $df = 1, 68$, $p < 0.005$; Table 2).

Trial identity had a significant impact on total fruit removal, with later trials having more fruit removal than trials conducted at the beginning of the season ($F = 24.31$, $df = 1, 68$, $p < .0001$). Ripeness index was not significant ($F = 0.032$, $df = 1, 68$, $p < 0.90$). However, there was a non-significant but very strong trend for an interaction between the ripeness index and trial ($F = 2.95$, $df = 2, 68$, $p < 0.06$; Table 2). Trials that began early in the season showed no clear correlation between ripeness index and fruit removal. However, for trials conducted during the latter portion of our study, fruit removal seemed to increase with ripeness index, suggesting that bushes with higher proportions of ripe fruits might have received higher frugivory.

Table 2. Fixed effects for a linear mixed model predicting total fruit removal per bush. Model: total fruit removal ~ stem color treatment + trial duration + trial + ripeness index + ripeness index:trial, random effects of bush + bush/stem.

fixed effect	num. df	den. df	F-value	p-value
intercept	1	68	117.447	<.0001
stem color (pink)	1	23	0.562	0.461
trial duration	1	68	0.471	0.495
trial	2	68	24.313	<.0001
ripeness index	1	68	0.032	0.858
ripeness index:trial	2	68	2.953	0.059

Discussion

The results of both our experiments suggest that the presence of both unripe and ripe fruits on a pokeweed plant might increase frugivory; however we cannot say this conclusively based on our data. In our first experiment, bushes that contained both ripe and unripe fruits showed a strong trend toward experiencing more frugivory than their counterparts with only ripe fruits. When we removed the potentially confounding variable of fruit count, that trend became a significant effect.

There are several possible explanations for why mixed displays would attract more frugivores than fully ripe displays. It is possible that bushes with a combination of ripe and unripe fruit are more easily seen by frugivores. If this is the case, increased frugivory would not be a result of any direct preference for the fruits of one bush over another. Rather, mixed displays would result in increased fruit removal due to a detection bias on the part of the frugivores. Schaefer et al. reported that components of fruiting displays other than the leaf and ripe fruit, such as an unripe fruit, provide more contrast against the display's background than the ripe fruit (2007).

Another, not mutually exclusive, explanation for the higher levels of frugivory on mixed displays is that the presence of unripe fruit might be providing valuable information to the frugivores and attracting them to the plant. Greig-Smith (1986) hypothesized that the presence of unripe fruits might indicate that ripe fruits on the same plant were fresh and unlikely to be damaged or desiccated.

By placing our fully ripe and partially ripe bushes side by side, we hoped to eliminate or drastically decrease any opportunity for our results to be based on detection bias. If unripe fruits do increase the conspicuousness of a pokeweed's display, once a frugivore has been drawn to the bush, the neighboring plant with only ripe fruits should be readily apparent as well. Furthermore, unripe pokeweed fruits turn from green to a reddish-purple before ripening to black. The green is similar in color to the plant's leaves, and the reddish-purple fruits are very similar in color to pokeweed's stems. This suggests that the unripe fruits of pokeweed are not adding any additional colors to the pokeweed display, and while they could be increasing the amount of each color present, we do not believe that their presence significantly alters the visual contrast or conspicuousness of the display Therefore, we suggest that if there is increased fruit removal on mixed displays of pokeweed, it would be due to a preference for their fruits rather than an inability to easily notice the fully ripe bushes.

However, if there is no real difference between fruit removal on mixed and fully ripe displays, we must look for other explanations for the asynchronous ripening that pokeweeds undergo. Since unripe fruits are less likely to be attacked by insects, asynchronous ripening could serve to protect a plant's reproductive investment from being destroyed (Mordenmoore & Willson, 1982). Asychronous ripening could also serve to increase the number and type of birds acting as seed dispersers by ensuring that not all fruits are removed at one time. This change in the quantity and type of seed dispersers could influence the seed shadow and reproductive success of the plant.

In our second experiment, we did not see a difference in fruit removal between our green and red stems. This indicates that birds are not using the color of our stems to make foraging decisions on an individual bush. It is likely that the additional color and contrast gained from a structurally mixed display like pokeweed's could play a role in attracting frugivores from a distance. The added conspicuousness of pokeweed's bright red stems could easily catch the eye of a bird and draw it to the plant. Once the birds are there, the stems might have little to no influence on fruit choice. This is contradictory to the results of several laboratory studies in which birds have shown differences in feeding based on the conspicuousness of the food against its background, even when the food is placed directly in front of them (Osorio et al., 1999; Schmidt et al., 2004). However, Honkavaara et al.'s study on fruit preference in redwings found no evidence of a role for contrast in short-range fruit choice (2004), which is consistent with our own experimental results.

While not finding a significant effect of structurally mixed displays, our second experiment did indicate that there is potentially an interaction between ripeness index and trial identity. This suggested that later in the season, fruit removal increased as the proportion of ripe fruits on the bush increased. Only one of our bushes had a ripeness index of 1, meaning it was fully ripe. The rest held both ripe and unripe fruits. As such, our results are most appropriately interpreted within our range of mixed displays. With this in mind, our data indicate that in the middle and end of the season, pokeweed mixed displays with high proportions of ripe fruit will receive more frugivory than bushes with mostly unripe fruit.

Birds might prefer bushes with large proportions of ripe fruit because it makes it easier for them to locate and eat the ripe fruit. Fully ripe fruit are generally more palatable and contain more nutrients than unripe fruit (Foster, 1977; Schaefer & Schaefer, 2006). Fruits may also contain more water per fruit when fully ripe (Foster, 1977; Poston & Middendorf, 1988). These characteristics make it more profitable for birds to choose ripe fruits over unripe fruits, and bushes with high numbers of ripe fruits would likely have increased foraging efficiency compared to bushes with few ripe fruits. Accessibility to ripe fruit has been shown to influence foraging choices and efficiency (Whelan & Willson, 1994; Schaefer & Schaefer, 2006).

If this trend, as well as the trend from our first experiment that mixed displays had higher fruit removal, are both biologically relevant and not simply a result of chance, it would suggest the possibility of a trade-off between ripening asynchronously in order to maintain fruit freshness and having a large proportion of ripe fruits in order to serve as an efficient foraging destination. Further work would be needed, first to determine if these trends are in fact true relationships, and second to accurately determine the number or percentage of unripe fruits necessary to signal the freshness of other fruits on the raceme while still allowing enough ripe fruits to allow efficient frugivory. Fuentes (1995) found that unripe fruits on the shrub *Pistacia terebinthus* decreased a bird's ability to access ripe fruits. Yet *Pistacia terebinthus* unripe fruit also increase the conspicuousness of the display, which suggests that, like the pokeweed, the presence of unripe fruit on this plant may influence frugivory in more than one way.

We did not see a correlation between ripeness index and frugivory at the beginning of our experiment. Early in the season, for instance late August or early September, juvenile birds would have little foraging experience. Both field and laboratory studies have shown differences in fruit choice and foraging between juvenile and adult birds. Juvenile American robins (*Turdus migratorius*) and redwings (*Turdus iliacus*) exhibit different color preferences than adults and may not have formed search images for ripe fruit (Willson, 1994; Honkavaara et al., 2004). American robin juveniles may not be able fully differentiate between ripe and unripe fruit, and they are less successful at picking up individual fruits and less skilled at fruit-foraging in general, compared to their adult counterparts (Vanderhoff & Eason, 2007). If juvenile frugivores begin the season with relatively low foraging skills and are less likely to reliably differentiate unripe and ripe fruits, they could forage indiscriminately on plants of varying ripeness. This could lead to a lack of correlation between plant ripeness and frugivory early in the season, such as we saw on our pokeweed plants. As the season progresses and juveniles gain more experience choosing and eating fruits, they might begin to prefer plants with higher ripeness indices, leading to a positive correlation between ripeness index and fruit removal.

In addition to our tentative findings regarding mixed displays, we also saw an unexpectedly large amount of deer frugivory on our pokeweed bushes, with deer responsible for 26% of the fruits removed. The majority of studies done on frugivory in temperate ecosystems focus on avian frugivores (Thompson & Willson, 1979; Sorensen, 1981; Willson, 1986; Gosper et al., 2005). While some work touches on the possibility of mammalian frugivory (Stiles, 1980; Willson & Melampy, 1983), surprisingly little work has been done on the proclivity of white-tailed deer to serve as seed-dispersers for plants that produce fleshy fruits (Lay, 1965; Myers et al., 2004; Williams & Ward, 2006).

We do not know if white-tailed deer can act as effective seed dispersers for pokeweed or if they render the seeds inviable during gut passage. Several studies have indicated that deer eat the fruit and disperse the seeds of the invasive honeysuckle (*Lonicera* spp.) (Vellend, 2002; Myers et al., 2004) and the invasive autumn olive (*Elaeagnus umbellata*) (Williams & Ward, 2006). There is some evidence that the likelihood of deer being able to disperse seeds increases as seed size decreases (Willson, 1993). The seeds of both autumn olive and honeysuckle are larger than those of pokeweed, suggesting that deer might be able to successfully disperse the seeds of pokeweed.

The months leading up to our study were unusually dry. While rainfall during the month of August was not low, the total precipitation for April through July at the Kellogg Biological Station Long-Term Ecological Research (LTER) site, which is close to our study site, was the lowest for a twenty year period. Dry conditions for much of the growing season could have significantly influenced the availability of food sources for white-tailed deer. If this is the case, deer might have consumed more pokeweed fruits than would be expected under normal conditions.

Future work is needed to determine exactly what role white-tailed deer play in the reproductive success and dispersal of pokeweed, as well as other fleshy fruit-producing plants. Our results indicate the potential for deer to have a significant impact either as a seed disperser or as a seed predator. The results of our study also suggest a possibility for avian frugivory on pokeweed to be influenced by temporally mixed displays, but in the context of our work, not by structurally mixed displays.

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