Dispersers and herbivores: the positive and negative effects of consumers on plants

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Dispersers and herbivores:
The positive and negative effects of consumers on plants

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for the degree of
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Dispersers and herbivores: The positive and negative effects of consumers on plants

Interactions between plants and the animals that use them for food are both ecologically and evolutionarily important. Here I document two contrasting plant-consumer interactions, one demonstrating important negative impacts of herbivores on plants and one examining plant traits to attract bird dispersers, whose consumption has positive effects on plants.

The goal of the first project was to explore the relative impact of a suite of consumers, including insects, small mammals, and large ungulates, on the fitness and population abundance of a dominant native perennial forb in western Montana, arrowleaf balsamroot (*Balsamorhiza sagittata*; Asteraceae), and to quantify how environmental context (elevation) may alter the strength of these interactions. Plant abundance and seed production decreased with increasing elevation. At all but the highest elevation site, inflorescence-feeding insect herbivores were abundant and quite damaging to balsamroot. These herbivores decreased balsamroot seed production by 20-330%, depending on elevation. In contrast, mammals had minimal impacts on balsamroot seed production. Whether reductions in seed production due to heavy herbivory translate to lower balsamroot recruitment was uncertain. Seed addition experiments indicated that balsamroot is not seed limited, but observational evidence suggested there may be a relationship between seed production and seedling recruitment. Overall, results indicated that inconspicuous insects have strong effects on balsamroot fitness, but the magnitude of these impacts change with elevation.

In the second project, I studied the role of unripe fruit color in attracting avian seed dispersers to ripe fruit of a neotropical tree, *Ardisia nigropunctata* (Myrsinaceae). Visual cues in fruit displays from foliage, accessory structures, and ripe fruit color are known to be important in attracting bird seed dispersers to ripe fruit, but the role of color in unripe fruit is relatively unstudied. Here, I examined this role by offering fruit of *A. nigropunctata* in bunches of mixed unripe and ripe fruit and bunches of all-ripe fruit. Contrary to expectation, birds were not attracted by colorful unripe fruit and instead removed more fruit from all-ripe bunches with the most fruit. Alternate explanations for color in unripe fruit due to sequential ripening are physiological constraint, flowering and pollination phenology, and warning coloration.
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The balsamroot herbivory project was greatly assisted by field help from John Steffen and Lorna McIntyre in the set-up and take-down. I am much obliged to Lorna also for counting half of the nearly 30,000 seeds! Discussions with Yvette Ortega greatly helped the overall project.

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I dedicate this thesis to my mom, Jan Amsberry, who gave me everything.
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CHAPTER ONE

Elevation-dependent impacts of consumers on a native perennial forb

Introduction

Herbivores reduce individual plant performance (see reviews by Crawley 1989a, Gagne 1990, Marquis 1992), and growing evidence indicates that they can also be important determinants of plant population dynamics (Louda and Potvin 1995, Maron 1998, Fagan and Bishop 2000). As our understanding of the overall impacts of herbivores on plants has increased over the last twenty years, so too has the realization that plant-herbivore interactions can be context-dependent. The impact of herbivores on plants can vary with individual abiotic factors such as soil moisture, soil quality, light availability, temperature, and productivity (see reviews by Louda 1989 and Marquis 1992) and with biotic conditions, such as associated plant or herbivore species composition or density (Futuyma and Wasserman 1980, Parker and Root 1981, Rand 1999). Thus the critical question concerning plant-consumer dynamics is no longer whether consumers have important impacts on plants but the conditions under which these impacts are manifest (Louda 1995).

Menge and Olson (1990) developed a heuristic framework for predicting how consumers’ effects on prey change with environmental stress. They proposed different models depending on whether the performance of prey (here: plants) or consumers (here: herbivores) is more greatly affected by stress. In their prey stress models, prey defenses are weakened relatively more than consumer activity under high stress. Thus, consumers will be more likely to control plant abundance in stressful environments. In general,
empirical studies of terrestrial plants support these prey stress models (Louda et al. 1987, Louda and Collinge 1992, Cobb et al. 1997). In contrast, consumer stress models predict that herbivorous consumers will be more inhibited by high environmental stress than their plant prey. In this case, consumers would have a greater effect on plants in low stress conditions.

A particularly interesting stress gradient over which plant abundance often varies is elevation. Changes in elevation create a complex natural system in which factors such as temperature, rain- and snow-fall, wind, soil stability, and growing season length all vary. Collectively, high elevation conditions are more stressful to plants, insects, and other herbivores than lower elevation conditions, although these organisms may differ in their response to stress. Several studies have examined plant-herbivore interactions at different elevations with mixed results (Randall 1986, Galen 1990, Kelly 1998, Scheidel and Bruelheide 2001). In general it seems that the effects of herbivores on plants decrease with increasing elevation, in contrast to the predictions of prey stress models but consistent with consumer stress model predictions.

Another factor that may determine a plant’s susceptibility to herbivory is the body size and mode of feeding of the herbivore. Plants are often attacked by a diverse suite of herbivore species, from invertebrates to large ungulates. Diverse feeding assemblages of herbivores may impose divergent selective pressures on plants (Juenger and Bergelson 1998). Some studies suggest that vertebrates have greater impacts on plants than invertebrates (Crawley 1989b, Hulme 1994, Palmisano and Fox 1997, Gomez and Zamora 2000, Sessions and Kelly 2001, Warner and Cushman 2002). However, a meta-analysis involving 246 comparisons of plant size with and without herbivores revealed
opposite results: invertebrate herbivores (insects, molluscs) had greater negative impacts on plant size than did vertebrate herbivores (gophers, rabbits, deer, elk, moose, geese; Bigger and Marvier 1998). Only two studies examined the relative impact of vertebrate and invertebrate herbivores on a focal plant’s reproduction; both studies found that despite their inconspicuous nature, invertebrates are more damaging than vertebrates (Strauss 1991, Ehrlein 1995).

How herbivore identity and environmental context interact to shape the outcome of plant-herbivore interactions is unclear. Few studies have compared the impacts of multiple herbivores in different ecological contexts (Palmisano and Fox 1997, Fletcher et al. 2001); more manipulative studies are needed to clarify how insect versus mammal impacts on plants vary, and how environmental gradients, such as elevation, mediate the relative impacts of these particular herbivore species on the focal plant’s fitness. Here, I studied the relative impacts of inflorescence-feeding insect and mammalian herbivores that consume entire flower heads on arrowleaf balsamroot (*Balsamorhiza sagittata* (Pursh) Nutt.; Asteraceae) reproduction over an altitudinal gradient. Arrowleaf balsamroot is a dominant, perennial forb that grows over a wide elevational range, and it is attacked by a variety of herbivores. I used a combination of natural observations, insect and ungulate herbivore exclosures, and seed addition plots at different elevations to tease apart the conditions under which the different herbivores had the greatest impact on balsamroot fitness and to examine how reductions in fecundity might influence plant recruitment. Prey stress models predict that if plants are more susceptible to stress than herbivores, then consumers would have a larger impact on plants in high stress conditions.
Materials and Methods

Study system

Arrowleaf balsamroot is a long-lived perennial forb with arrow-shaped, pale green, pubescent leaves and large, usually solitary inflorescences composed of showy, golden-yellow ray flowers. Hereafter I will use “flower head” to refer to balsamroot’s head inflorescence typical of the family Asteraceae. In western Montana, balsamroot germinates in early spring, flowers in May, and begins to set seed in June. It reproduces solely by seeds, which are formed after pollination by a small number of solitary bees, including Bombus, Osmia, Andrena, and Synhalonia (Apidae; James Cane, personal communication).

Balsamroot is a major component of the arid native bunchgrass communities in western Montana (Stubbendieck et al. 1986). Balsamroot grows over a broad altitudinal gradient (600-2400 m) on steep slopes with south to southwest or southeast-facing aspects. It also has a wide geographical distribution across western North America from California to British Columbia (Young and Evans 1978).

Balsamroot is an ideal plant with which to examine the relative impacts of different types of herbivores on plant reproduction because it experiences high levels of herbivory. Balsamroot is attacked by a variety of inconspicuous inflorescence-feeding insect herbivores. At least one species of Lepidopteran larvae (family Tortricidae), as well as several species of Dipteran larvae (one Cecidomyiidae species and at least two species of Tephritidae), can be found foraging within the heads (Amsberry, personal observation). Moreover, plants lose many whole flower heads to mammalian herbivores.
Its seed and flower heads appear to incur heavy browsing from ungulates such as deer, elk, horses, and cattle (USDA Forest Service 1937). Observations prior to the study revealed heavy damage by both insects and by mammalian herbivores which I postulated to be ungulates including deer, bighorn sheep, and elk. These herbivory patterns, in combination with the fact that balsamroot has a wide elevational distribution, make it an excellent system in which to test context-dependent changes in herbivore impacts.

2002 field study

In the summer of 2002 I conducted an observational study to determine the potential impacts of insects and mammals on balsamroot reproduction. I gathered data from 300 plants at six sites, all above Skalkaho Creek in the Bitterroot National Forest outside of Hamilton, MT. Two of these sites were re-used in 2003. I measured larval abundance by collecting and dissecting three flower heads from each of twenty plants at the six sites. I counted seedlings within 0.5 m around fifty random adult plants at the six sites; I considered seedlings to consist of plants with only one leaf less than 5 cm long. I also censused the number of flower heads per plant, estimated the number of flower heads eaten by mammals, and counted the number of seeds per flower head per plant. Seeds were categorized as follows: “good” if they were filled with an embryo; “eaten” by larvae if they had a hole bored into them and/or insect frass; and “aborted” if they were a shriveled mass that did not develop.
2003 field study

The bulk of this study was conducted during summer 2003 at four sites across western Montana that varied in elevation. The lowest elevation site was located at 1100 m in the North Hills Open Space area near Missoula, MT. The next site was located at 1385 m near Petty Pasture in Lolo National Forest outside of Alberton, MT. The two highest elevation sites used were both located above Skalkaho Creek in the Bitterroot National Forest (same as 2002). One of these sites was at 1525 m, and the highest elevation site was at 1825 m. These two highest sites were about eight km apart, and they were about 100 km from each of the other two sites. The 1100 m and 1385 m sites were about fifty km apart. Sites were chosen because they were similar in vegetation composition (e.g. similar percent cover of the invasive plant spotted knapweed), slope, and aspect (south to southwest or southeast-facing).

Plant abundance surveys.

I censused balsamroot populations to determine how plant abundance varied by site. At each site, I counted the number of flowering and non-flowering plants along eight randomly-placed 50 m x 1 m belt transects at the end of May when balsamroot was flowering. Transects were placed 10 m apart and covered the extent of the study areas used. Non-flowering plants were included in this count if they had at least two leaves longer than 10 cm. To determine the extent of seedling recruitment into study populations, at each site I censused recruits within 0.5 m around fifty randomly-selected adult balsamroot plants, as in 2002. Recruits were defined as plants possessing only one leaf no more than 5 cm long.
Surveys of inflorescence-feeding insects.

To measure insect larval abundance, to determine how abundance changed seasonally, and to assess the effectiveness of insecticide treatment in excluding herbivory on balsamroot flowers, I conducted weekly surveys of heads from 40 marked plants at each site. Half of the plants at each site were sprayed weekly from late April through the end of June with a small amount of the insecticide Orthene™ directed solely at the flower heads. Orthene™ containing 97% active ingredient acephate (Valent Corporation, Walnut Creek, CA) is a broad spectrum insecticide, which has been used in other studies to effectively reduce numbers of Lepidopteran and other larvae (Kelly and Dyer 2002). It is not toxic to many crop plants (Worthing 1987). I used 0.81 g per L of Orthene™ dissolved in water, within the recommended range to control aphids, thrips, and beetles on outdoor floral crops.

Each week at each site, I harvested one head from each of the 40 plants, 20 control and 20 sprayed with insecticide, and recorded the type and number of larvae found within the head. This destructive harvest allowed me to determine if the insecticide successfully reduced larval abundance within heads. I also recorded the phenological stage of each head—i.e. bud (neither ray nor disk flowers developed), flowering (at least ray flowers developed), or senesced (both ray and disk flowers dried or fallen off). If the head was flowering, I further recorded the stage of the disk flowers (undeveloped, receptive, senesced).
Experimental suppression of herbivory on plants.

To tease apart the relative impacts of inflorescence-feeding insect herbivores and foliage and flower-feeding ungulate herbivores on balsamroot reproduction, I factorially excluded insects and/or ungulates from individual plants at each site. I selected and marked 120 balsamroot plants comparable in size and head number at each of the four sites and randomly assigned one of the four treatment combinations to 30 plants each. To exclude the insects, every week I sprayed flower heads of designated plants with a small amount of the insecticide Orthene™, as described above. I sprayed the heads of the other plants with water as a control for the small amount of water being added with the insecticide. These plants were left intact until the end of the season to determine seed production with and without insect herbivores.

For the ungulate exclosures, I constructed wire cages that I placed around individual plants. Cages were made of 2.5 cm mesh poultry netting formed into cylinders (60 cm in diameter and 90 cm in height) that were closed at the top. These cages allowed enough space for enclosed balsamroot plants to grow throughout the season. Each cage was attached to the ground with metal sod staples.

For the 120 study plants at each site, I conducted initial censuses at the beginning of the flowering period, ranging from 9 May at the 1100 m site to 21 May at the 1825 m site; at the end of the growing season (8 to 22 July), I conducted final censuses. To determine the fates of flower heads, I categorized heads into three groups: aborted, if heads were a shriveled mass that never developed full flowers or seeds; snipped, detected by the presence of a flowering stalk missing a flower or seed head (assumed to be eaten

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by mammals); and good, if heads had the potential to produce seeds. For the censuses, I recorded the number and conditions of flower heads for each plant.

To ensure that mature seeds did not disperse from flower heads, starting on 9 June at the 1100 m site, I covered all heads on each focal plant with fine mesh nylon tulle (a.k.a. bridal veil). When heads were fully matured, I harvested all the heads from each plant, and in the laboratory, I counted the number of viable seeds per head for each plant. I used a firmness index to detect presence of an embryo inside to determine if a seed was filled and therefore likely viable. I counted the number of good (viable) seeds from each head separately for up to 10 heads per plant. Data from 2002 indicated that ten was a reliable estimate of the true average number of good seeds per head. Thus for the 25% of plants that had more than 10 heads, I used the average per head (calculated from the ten I had counted) multiplied by the number of heads to estimate the total number of seeds produced by the plant. I also weighed the seeds to get an average mass per good seed per plant.

Seed addition.

To examine how variation in seed production might influence the magnitude of plant recruitment, I established 0.5 m x 0.5 m plots in the first summer (August 2002) to which I added seeds at five densities—0, 13, 25, 50, and 100. The latter densities well exceeded natural seeding rates (as determined in my seed production counts) and thus provided an assessment of seed limitation in this species. I used five plots as a block replicated six times at each of the two Skalkaho sites, 1525 m and 1825 m, where I had access in 2002 and 2003. Plots were placed away from adult balsamroot plants, though
in the same general areas. Plots were at least two meters apart, and blocks were at least ten meters apart. The following summer after seeds were added, I surveyed the plots for seedlings every few weeks from 13 April to 22 July 2003. I marked any balsamroot recruits I found with colored plastic toothpicks to keep track of their fates over time.

Analyses.

All statistical analyses were performed in SYSTAT 10. I performed regressions of elevation on balsamroot adult and seedling abundances. To examine how experimental manipulations influenced the number of Lepidopteran larvae per flower head, the numbers of heads per plant, the average number of good seeds per head, the total seeds per plant, and the average weight per seed, I conducted separate two-way ANOVAs on each response variable using a General Linear Model with elevation and spraying treatment as factors. I also performed regressions of elevation and Lepidopteran abundance on the percent increase in seed production when insects were excluded, and of the number of seeds versus average seed weight per plant. One-way ANOVAs were used to analyze seed densities on seedling abundance at the two seed addition sites. Finally, I calculated a Pearson correlation coefficient for site averages of seed production per plant and recruits per plant.

Since analysis showed that caging had no effect on the total number of heads (see Results) per plant, I combined caged and uncaged plants sprayed with insecticide (hereafter called sprayed) and caged and uncaged control plants (control) to estimate the influence of insect herbivores on seed production.
Despite ungulate exclusion, many caged and uncaged plants were missing seed heads. Observations, including scat on vegetation and the way in which the heads were snipped, indicated that small mammals were the likely culprits of late season seed head predation. Since small mammals were not affected by caging, I estimated their effect on seed production in the following way. I added together the number of heads I harvested (for which seeds were counted) plus the number of stalks with heads missing (the "snipped" category) and multiplied this total number of heads by the average number of good seeds per head for control plants. This gave me an estimate of the seed production if small mammals had been excluded, but not insects. I then calculated the percent increase in seed production if small mammals had been excluded.

**Results**

**2002 field study**

A variety of insects were commonly found in balsamroot flower heads. These included late instar larvae and pupal cases of tephritid and cecidomiid flies and lepidopteran larvae (family Tortricidae). Since the lepidopteran larvae were by far the largest, most abundant, and most damaging herbivores in flower heads, hereafter I focus only on these insect herbivores. Of 902 seed heads sampled, 610 or 68% had evidence of damage by lepidopteran larvae. Lepidopteran larval abundance was $1.7 \pm \text{SEM} 0.1$ per head. Plants produced, on average, only $2.9 \pm \text{SEM} 0.4$ good seeds per head, whereas on average $4.3 \pm \text{SEM} 0.3$ seeds per head were eaten by larvae and $20.6 \pm \text{SEM} 1.0$ were aborted. Total good seed production per plant averaged $21.9 \pm \text{SEM} 3.4$ across all six sites.
Furthermore, 120 individual plants at the six sites lost an average 5.9 ± SEM 0.6 of their flower and seed heads to mammalian herbivores. This nearly equaled the number of good seed heads remaining, 7.1 ± SEM 0.6.

2003 field study

Plant and insect abundance surveys.

Balsamroot adult and seedling abundance decreased with increasing elevation ($R^2=0.948$, $F_{1,2}=36.548$, $P=0.026$ for adults; $R^2=0.865$, $F_{1,2}=12.831$, $P=0.070$ for seedlings; Fig. 1). All sites except the lowest elevation had approximately three times more flowering than non-flowering balsamroot plants. In keeping with this exception, the lowest elevation site had significantly more recruits than the other sites.

Weekly larval surveys revealed that spraying flower heads with insecticide effectively reduced the prevalence of lepidopteran larvae (Fig. 2). Analysis of the maximum number of larvae at each site showed that there were significantly fewer lepidopteran larvae in sprayed plants at each site ($F_{1,156}=11.365$, $P=0.001$). Site elevation also marginally affected abundance ($F_{1,156}=3.732$, $P=0.055$), and larval abundance peaked at different times in the season depending on elevation (Fig. 2).

Effects of herbivores on balsamroot performance.

As in 2002, insect larvae had a substantial impact on balsamroot seed production. Experimental suppression of seed-feeding insects resulted in 44 - 660% gains in seed production per head and 20 - 330% increases in total seeds produced per plant compared to control plants. Insecticide-treated plants produced significantly more
seeds per head than control plants, and total per capita fecundity was also higher for sprayed versus unsprayed plants (Table 1; Fig. 3). In addition, plant reproductive success differed significantly by elevation (Table 1). However, the effect of the insecticide treatment depended on elevation (Table 1); suppression of herbivores had minimal impacts on plant fecundity at the high elevation site (post-hoc contrast, $F_{1,111}=0.507$, $p=0.478$).

The percent increase in seed production when insects were excluded (calculated as $\frac{\text{[(Sprayed-Control)/Control]} \times 100}{\text{-i.e. the percent difference between control and sprayed plants-}}$ did not follow an elevational trend ($R^2=0.051$, $F_{1,2}=0.108$, $P=0.774$), but it was highly affected by the number of lepidopteran larvae in flower heads ($R^2=0.920$, $F_{1,2}=23.000$, $P=0.041$; Fig. 4).

Insect herbivory had no effect on seed weight; seeds from control and sprayed plants did not differ significantly in weight ($F_{1,212}=1.651$, $P=0.200$). However, seed weight was significantly affected by elevation ($F_{1,212}=19.263$, $P<0.001$). There was no relationship between total seeds per plant and average weight per seed across all sites ($R^2=0.012$, $F_{1,214}=2.668$, $P=0.104$). Thus elevation had the largest effect on seed weight, as compared to seed number or treatment (control or sprayed).

At the end of the growing season, total head number and fate of flower heads (good, snipped, aborted) significantly differed by elevation (two-way ANOVA, $F_{1,481}=13.065$, $P<0.001$; Fig. 5), but not by spraying ($F_{1,481}=0.201$, $P=0.654$). Furthermore, caging did not significantly reduce head loss (three-way ANOVA, $F_{1,477}=0.881$, $P=0.348$), indicating that ungulates had little impact on plant performance.

Overall, 13% of heads from both caged and uncaged plants were lost due to mammalian
snipping (likely small mammals), which corresponded to minimal effects of mammalian snipping on total seed production (3-31%).

Seed addition.

Seed addition plots had extremely low recruitment (Fig. 6), despite the high density of seeds added. In fact, at the 1825 m site only four plots (of 29) had seedling emergence. At the 1525 m site, 17 plots (of 30) had seedlings, though only nine plots had seedlings that survived till late June, when natural senescence began. The natural recruitment around adult plants for these sites (Fig. 1) was also very low: 0.4 per m$^2$ in 2002 and 2.4 per m$^2$ in 2003 for the 1525 m site; and 0.8 m$^2$ in 2002 and 1.5 per m$^2$ in 2003 for the 1825 m site. Because recruitment levels in all plots were universally low, I could discern no distinct relationship between greater numbers of seeds added per plot and greater seedling recruitment ($F_{4,25}=1.801$, $P=0.160$ for the 1525 m site; $F_{4,24}=1.252$, $P=0.316$ for the 1825 m site).

Sites with higher seed production generally had more naturally-occurring recruits per plant, but this effect was not significant ($r=0.880$, $P=0.120$; Fig. 7). Sites with higher natural recruitment had more adult plants (Fig. 1).

Discussion

Inconspicuous inflorescence-feeding insect herbivores were abundant and had significant impacts on balsamroot seed production. Spraying with insecticide, which suppressed larval abundance, significantly increased the average number of seeds per head and the total seed production per plant at three of the four sites (Fig. 3); thus the
effects of the insect herbivores varied by elevation. At the highest elevation site, insect herbivores had no effect on seed production. In addition, ungulates did not have an impact on seed production at any site.

Flower heads had high infestation rates by insects. Across all sites, 79% (range: 61 - 95%) of heads of control plants, which allowed access to insects, showed some damage. By comparison, 17% (range: 10 - 29%) of sprayed heads showed evidence of insect damage. The sprayed plants are thus a conservative estimate of the insect effect since insecticide treatment was not 100% effective. The sprayed plants exhibited up to 330% increases in total seed production when insects were suppressed, and these increases were tightly linked to lepidopteran abundance (Fig. 4).

This study adds to the growing number that has shown that inconspicuous flower and seed-feeding insects can have substantial impacts on plant fitness (Louda 1982, Louda and Potvin 1995, Maron 1998, Carson and Root 2000, Kelly and Dyer 2002, Maron et al. 2002). Such herbivore pressure on balsamroot is likely chronic, since observational data from 2002 showed high numbers of eaten seeds, in addition to the high levels experimentally shown in 2003.

Flower head loss in 2002 was substantial, averaging 43% (range: 5 - 83%) of non-aborted heads, and initial observations suggested ungulates were the primary grazers. However, in contrast to these initial results, ungulates had minimal impacts on balsamroot fitness in 2003. While ungulates can damage young balsamroot leaves and buds early in the growing season (Amsberry, personal observation), predation on flower heads did not appear to be more important than bud abortion. Balsamroot plants emerged from the ground in the spring with flower buds already present, but many of these heads
never developed (especially at the 1385 m site; Fig. 5). It is likely that heads lost to ungulates would have been aborted later anyway, resulting in no net loss of heads to these herbivores.

Small mammals were likely responsible for late season seed head removals, as suggested by several lines of evidence. I observed signs of mice (*Peromyscus* species), chipmunks (*Tamias* species), pocket gophers (*Thomomys talpoides*), and ground squirrels (*Spermophilus* species) at the study sites. For example, I occasionally noticed mouse scat on balsamroot leaves. In addition, the sharp angle of incision on the flowering stalk from which the head was removed was typical of small mammals rather than large ungulates that lack upper incisors. Story et al. (1995) described similar methods of identifying herbivore perpetrators based on damage type. Finally, Everett et al. (1978) reported that deer mice preferentially eat balsamroot seeds. Small mammal herbivory occurred later in the growing season, after the plants had invested more energy in seed maturation. I observed significant seed head removals about the time the seeds were maturing; thus it was likely that small mammals targeted the seeds at this crucial time in balsamroot's reproduction.

Analysis of the relative impacts of small mammals and insects suggested that eliminating small mammals would have a much lower (3 - 31% depending on site) increase in seed production per plant than that observed when insects were excluded (20 - 330%; Fig. 3). This observation that insects had a stronger effect on seed production runs counter to the generally-held belief that large vertebrates should have a higher impact than insects (Crawley 1989b, Hulme 1994, Palmisano and Fox 1997, Gomez and Zamora 2000, Sessions and Kelly 2001, Warner and Cushman 2002). However, my results are
consistent with some studies that have found invertebrates to have greater impacts on plant performance than mammals (Strauss 1991, Ehrlen 1995, Bigger and Marvier 1998). In this study, the insects’ impacts were probably strong because of high rates of infestation and because balsamroot often produced very few viable seeds even when insects were excluded.

Elevation affected the abundance of balsamroot (Fig. 1) and to a lesser degree the abundance of lepidopteran larvae (Fig. 2). The decrease in abundance of these taxa at the highest site (1825 m) indicated more stressful abiotic conditions there for these species. Certainly there was a delayed and shorter growing season at this high elevation site, as plants did not reach a similar phenological stage until three weeks after the lowest site (1100 m). Also, adult plants at the high site were smaller and generally produced fewer, lighter seeds than at the other sites.

The high elevation site was the only site at which insects did not have a significant impact on balsamroot seed production. This finding contradicts the prediction of prey stress models (Menge and Olson 1990) that consumers should be less susceptible to abiotic stress than their plant prey, translating to greater impacts in more stressful contexts. Possible reasons for this are: (1) low plant abundance drove insect abundance, (2) consumers were more stressed than plants, or (3) both plants and insects were highly affected by stress, reducing the general intensity of their interactions.

However, the finding of this study agrees with the predictions of consumer stress models, as well as most studies that have examined the patterns of herbivore impact across elevational gradients. For example, ungulate grazing, aphid herbivory, and the negative impacts of these consumers on seed set decrease from the lower to upper limit of
the elevational distribution of a *Polemonium viscosum* (alpine skypilot, Polemoniaceae) population (Galen 1990). Similarly, mollusc herbivore damage on six montane Asteraceae species generally decreases with increasing elevation (Scheidel and Bruelheide 2001). In contrast, a few studies show increased herbivory at high elevation. Predators have a greater impact on *Solidago macrophylla* (large-leaf goldenrod, Asteraceae) seeds at higher elevations due to equal numbers of Dipteran seed predators across the gradient but fewer total florets at higher elevations (Kelly 1998). Finally, seed-eating moth larvae are most damaging to *Juncus squarrosus* (heath rush, Juncaceae) at middle elevations (Randall 1986). At low altitudes parasitoids keep moth populations low; at high elevations moths are limited by physical factors. The latter two studies show the importance of determining relative densities and susceptibilities of herbivores and plants to environmental stress.

The 1385 m site deserves special attention because it did not follow all patterns observed at the other three sites. At this site, I observed the highest change in good head number over the growing season, the lowest seed production, the heaviest seeds, and the highest number of larvae. The high number of larvae was correlated with low seed production in 2003 (Fig. 4), but balsamroot was abundant at this site. Most of the decrease in the number of good flower heads at this site was due to bud abortion (Fig. 5), but it was unclear why abortion was higher at this site than elsewhere.

Balsamroot appears to naturally produce few seeds per flower head. In 2002, control plants produced, on average, only 3 seeds per head; in 2003, the average for control plants was 7 seeds per head across all sites. 2002 data also indicated that balsamroot had a high (75%) seed abortion rate; high ovule abortion rates have been
noted in another study (Maze et al. 1990). The high seed abortion rate may be because of the potentially strong selective pressure generated by the head loss and seed predation. That is, if many seeds were eaten consistently over time, selection would favor low plant investment in viable seeds per head.

If adding seeds at higher densities results in higher seedling recruitment, populations are seed limited—i.e. populations are more limited by the number of seeds produced rather than sites favorable for germination. Seed addition experiments can be used to infer population-level impacts of consumers that reduce seed production (Turnbull et al. 2000). From a curve of the relationship between the number of seeds added and the resulting seedlings, the decrease in seed production due to herbivores can be extrapolated onto the subsequent reduction in seedling numbers. Such population-level impacts of herbivores are just beginning to be appreciated (Louda and Potvin 1995, Maron 1998, Maron and Gardner 2000). The low recruitment throughout the seed addition plots at the 1525 m and 1825 m sites (Fig. 6) suggests that balsamroot at these sites is not strongly seed limited. Seed dormancy, as shown by seedlings in the plots at the 1525 m site with zero seeds added, may have reduced the evidence for seed limitation. In addition, small mammals may have eaten some of the added seeds. Still, even if consumers decreased per capita seed output from a density of 400 per m$^2$ to 0 per m$^2$, no significant difference in recruitment would be observed in these populations. However, these results should be interpreted with caution as they represent recruitment in a particular year. The rough correlation between sites with higher total seed production and higher natural recruitment per plant (Fig. 7), on the other hand, provided some evidence for seed limitation across sites and suggests that consumers that significantly
reduce seed production could affect balsamroot abundance. The fact that higher recruitment in 2003 (driven by seed production in previous years) was associated with higher seed production in the same year suggested consistency of seed production across years. In fact, seed production was fairly similar for both years at the two sites where I measured it (total seed production per control plant—1525 m site: 2002=64, 2003=60; 1825 m site: 2002=12, 2003=26).

Since arrowleaf balsamroot is a dominant species in native bunchgrass communities across the Rocky Mountains, it is obviously successful even with heavy herbivore pressure. Balsamroot may be long-lived (Stubbendieck et al. 1986), and this may account for some of its success. For a long-lived adult plant to successfully replace itself with productive progeny, i.e. have high fitness, it may only need to have one good year in every five or ten over the course of its lifetime. As mentioned previously, balsamroot plants invest relatively little energy in seed production per head. Because of the high probability of loss to insects and/or small mammals, the plant’s strategy may be to invest heavily only in certain years with favorable conditions. Following the long-term dynamics of this plant, which is an important member of its community, is key to deciphering its success.

This study was unique in quantifying the relative impacts of different herbivore types on seed production across an elevational gradient. In this case, it appeared that insects had a larger effect on seed production than mammals at all but the highest elevation site. At the highest site, neither insects nor mammals had a strong effect. Thus there was only minimal evidence for a shift in relative importance of herbivore type.
driven by elevational changes; rather, the effect of elevational stress was to reduce impacts of any herbivore.
Literature cited


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**Figure Legends**

Fig. 1. Mean (± 1 SEM) density of adult (triangles) and seedling (squares) balsamroot plants at the four different elevation sites.

Fig. 2. Mean number (± 1 SEM) of Lepidopteran larvae per flower head in control (triangles) and sprayed (squares) plants throughout the flowering season. (N=20 heads each)

Fig. 3. Mean (+ 1 SEM) viable seeds (A) per head and (B) per plant on sprayed (open bars) and control (closed bars) plants (N=60). Percentages above bars indicate the increase in seed production due to herbivore suppression.

Fig. 4. The relationship between the maximum average number of Lepidopteran larvae per flower head and the percent increase in seed production due to herbivore suppression. Corresponding site elevations listed next to data points.

Fig. 5. Number of good, snipped, and aborted flower heads at the end of the growing season for control (C) and sprayed (S) plants.

Fig. 6. Mean (+ 1 SEM) cumulative number of seedlings that emerged from seed addition plots.

Fig. 7. The correlation between the average number of total seeds per control plant at a site and the average recruits per plant. Corresponding site elevations listed next to data points.
Table 1. Effect of elevation and insect herbivore suppression on (A) average seeds per head and (B) total seeds per plant

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</table>
Fig. 1

![Graph showing the relationship between elevation and plant density and recruit density.](image-url)
Fig. 2

- 1100 m
- 1385 m
- 1625 m
- 1825 m

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Fig. 3

(A)

(B)

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Fig. 5

![Graph showing number of heads per plant at different site elevations (1100 m, 1385 m, 1525 m, 1825 m). The graph has bars for 'good', 'snipped', and 'aborted'.]
Fig. 6

1525 m

1825 m

# seeds added per plot

# seedlings per plot

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CHAPTER TWO

Do colorful unripe fruits attract avian seed dispersers?

Introduction

Because seed dispersal is a crucial component of plant demography, plants have evolved many strategies to increase dispersal efficiency. Fruits, for example, attract a variety of animals to facilitate seed dispersal. Birds are particularly important seed dispersers, and because birds have good vision plants have evolved various visual signals to attract them. For example, foliage color surrounding fruit displays may enhance fruit conspicuousness to dispersers (Stiles 1982, Willson and Whelan 1990, Burns and Dalen 2002), and colored structures holding the fruit infructescences may also augment visibility (Stiles 1982, Willson and Thompson 1982). In addition, ripe fruit color itself may be important in attracting dispersers. Frugivorous birds often prefer feeding on ripe red and black fruits over green, yellow, or blue (Wheelwright and Janson 1985, Willson and Whelan 1990), although red and black dull-colored ripened fruits may be less noticeable. The darkened fruit may be necessary for absorbing radiation to raise the fruit temperature required for the ripening process (Janzen 1983). In plants producing dull-colored ripe fruits, it may be particularly important to have other visual signals for attracting dispersers, especially in tropical forest understories which are often very dark.

Fruits often change color as they ripen, which may serve as a signal to dispersers, and the preripe or unripe fruits themselves may be colorful. Many plants do not ripen fruit in infructescences all at once, and this often results in fruit bunches of differently-colored fruits. Stiles (1982) suggested that plants with sequential ripening may use
colorful or contrastingly-colored unripe fruit as a “preripening fruit flag”—that is, as an advertising signal for the ripe fruit. Colorful unripe fruit or the contrast of unripe and ripe fruit may be more noticeable to a bird disperser. It could also alert resident frugivores that more ripe fruit will become available over time and thus foster traplining. This behavior has been described for pollinating hummingbirds and euglossine bees, who monitor plants that sequentially open nectar-producing flowers (Stiles 1982). The preripening fruit flag hypothesis predicts that colorful unripe fruit attract bird dispersers.

Several studies have shown that multi-colored fruit displays resulting from fruit color polymorphisms or colored accessory structures increase fruit consumption rates by avian dispersers (Willson and Melampy 1983, Wheelwright and Janson 1985, Whelan and Willson 1994). Little attention has been focused on the role of colorful unripe fruit due to sequential ripening as a fruit flag, although this idea was proposed twenty years ago (Stiles 1982). The study conducted by Willson and Melampy (1983) addressed the sequential ripening process, though not explicitly stating it, by examining bicolored fruit displays of immature and ripe fruit. At the end of their study, they proposed that further similar field experiments should be conducted in many other study areas to test the generality of their results.

Here I test the preripening fruit flag hypothesis that contrastingly-colored unripe fruits attract avian seed dispersers in the neotropical tree, *Ardisia nigropunctata* Oerst. (Myrsinaceae). Given a plant that ripens its fruit asynchronously, the prediction is that if the unripe fruits serve to attract bird seed dispersers, then visitation and removal rates of ripe fruit should be higher in variegated fruit bunches compared to all-ripe bunches.
**Ardisia nigropunctata Natural History**

*Ardisia nigropunctata* Oerst. (Myrsinaceae) is a neotropical tree of second-growth forests. *Ardisia* has a thin trunk (about 2.5 cm dbh) and averages about 4 meters in height (Amsberry, unpublished data). The ripening of its drupe fruits is staggered, and its non-odorous infructescence bunches produced in the dry season (January – March) consist of a medley of colors ranging from white to pink to red to a ripened dark red. Trees have multiple bunches at once, and the number of fruits in a bunch is highly variable. A random sample of 34 natural bunches yielded an average total of 130 ± 16 fruits; however the range was 6 to 327 (Amsberry, unpublished data). The average ratio of fruit colors in the sample was 3.8 white to 1.2 pink to 1 red. The deep-red ripe fruits of *Ardisia* are on average 6.5 mm in diameter, and their water to sugar composition is 15:1 (Alex Gilman, unpublished data). The seeds are quite large compared to the fruit size; they average 3.7 mm in diameter. The mass of the fruit is about 0.16 g (not dried), and the seeds weigh about 0.04 g. To date, there are no known published studies on *Ardisia* fruit displays.

**Methods**

This study was conducted at La Selva Biological Station, Heredia Province, Costa Rica between 15 and 28 February 2003. La Selva is a typical lowland moist tropical rainforest (4 m annual rainfall; elevation 60 m). I studied *Ardisia* plants in several secondary forest sections about 10 – 12 years of age throughout La Selva. Many frugivorous birds inhabit areas where *Ardisia* grows at La Selva (Levey 1988). Birds...
commonly in the vicinity of *Ardisia* include tanagers, manakins, flycatchers, catbirds, and robins. Several species were observed eating *Ardisia* fruits.

To test the preripening fruit flag hypothesis, I established three experimental fruit bunch types: (1) 20 ripe (deep red) and 20 unripe (white and pink) fruits (hereafter R/U); (2) 20 ripe fruits (hereafter R); and (3) 40 ripe fruits (hereafter 2R; Table 1a). This design enabled me to compare removal rates of ripe fruit based on the same number of ripe fruits with and without unripe fruits (R/U versus R), as well as comparing removal rates from bunches with the same number of total fruits (R/U versus 2R). In other words, having two controls (R, 2R) allowed me to distinguish if birds favor multi-colored displays because there were more total fruits present or because colorful unripe fruits are attractants to birds. A comparison of the R and 2R bunches allowed me to test any difference in removal rates based on the total number of ripe fruits. The preripening fruit flag hypothesis predicts that the highest removal rates would be from the R/U bunch types.

I harvested fruit bunches from local parent trees and removed fruits by hand to leave the designated number of fruits. I presented the experimental fruit bunches to bird dispersers by tethering them to non-*Ardisia* trees in a standard way. By using *Ardisia* bunches tethered onto other tree species, I was testing birds' abilities to find fruits regardless of other signals (e.g. *Ardisia* foliage search image). *Ardisia* naturally occurs in the general areas I chose for study, but I used experimental tree locations not in the immediate vicinity of *Ardisia*. I attached 30 cm long dowel rods (rubbed in the mud to remove any odor or stark color) to the trees with duct tape at a height of about 1.5 meters, within the natural bunch height range. To attach the experimental bunches to the dowel
rods, I used green plastic-coated twist ties. While these displays were very artificial, which can affect bird visitation (Moermond and Denslow 1983), they were consistent among treatments. I put up the bunches at dawn (0600) and returned about every four hours (1000, 1400) until dusk (1800) to count the number of remaining fruits. I assumed any fruits removed were taken by birds. I did not observe any evidence that animals other than birds were eating *Ardisia* fruits.

I used a latin square crossover design (Feinsinger et al. 1991) to present the experimental fruit bunches at the tree locations. In this design, each treatment is tested once on each unit and once in each period within a sequence (Petersen 1985). Here my treatments were bunch type (R/U, R, 2R), and the experimental unit was the tree location where bunches were placed (Table 1b). I used this design because it allowed me to rotate experimental bunch treatments through a particular tree unit to reduce location effects. For my experimental units, I chose three non-*Ardisia* trees about one meter from a trail. Trees within the same block were at least five meters apart, and blocks were separated by at least 20 meters.

At the onset of the experiment, I randomly assigned one of the experimental bunch types (R/U, R, 2R) to each of the three trees in a block. Thus, at a given block at a given time, there was simultaneous presentation of the three treatments. I then rotated the treatments in a randomly chosen sequence (Table 1b). I allowed two days between each fruit presentation at tree locations to minimize carryover effects of avian learning—that is, to prevent the birds from developing an association between fruit availability and a particular tree location. Thus carryover effects were not included in the analysis. I
established 12 blocks, but I only used 4 blocks on a given day to allow for the two-day resting period.

In order to observe bird behavior at fruit bunches, I video-recorded three fruit bunches each day for 8 hours (approximately 0600 – 1400) using three Sony camcorder cameras, one for each treatment within one block. These tapes allowed identification of visiting frugivores as well as observe visitation frequency, duration, and number of fruits eaten per visit. Cameras were placed four to seven meters from the experimental fruit bunches on mini-tripods to steady them. They were covered with camouflage sleeves to make them less noticeable to potential bird visitors.

Data were analyzed in Systat 10 using an ANOVA model, following Feinsinger et al. 1991 and Petersen 1985. Factors were bunch type, block, time period nested within block, and tree location nested within block; the response variable was the number of fruit removed by the end of the day (1800). Post-hoc Fisher's Least-Significant-Difference tests were used to compare bunch type differences in a pairwise manner. A one-way ANOVA model of bunch type as the factor and number of fruits eaten per visit was used to analyze the video results.

I used the actual number of fruits removed instead of the percent removed because number is more important from the plant's perspective. That is, number of fruits removed represents fitness better than the percent removed. In only two cases of 36 were all ripe fruits taken from R/U bunches, and in only six cases of 36 were all ripe fruits taken from R bunches. Thus, the maximum fruit removal was rarely reached and further justifies the comparison based on number rather than percent.
Results

The preripening fruit flag hypothesis predicts that removals would be greatest under the R/U treatment. Bunch type did have a significant effect on removal rates (Table 2, Fig. 1). However, contrary to the hypothesis, there was no difference between the R and R/U treatments (post-hoc contrast P=0.399). In fact, the total number of ripe fruits removed by dusk was significantly highest for the 2R treatments (post-hoc contrasts P=0.001 for 2R vs. R; P<0.001 for 2R vs. R/U). Block also significantly affected the number of fruits removed (Table 2), but time period nested within block and tree nested within block did not (Table 2).

The number of ripe fruits removed from all treatments was highest between 0600 and 1000, followed by those removed between 1000 and 1400, and last between 1400 and 1800 (Fig. 1).

From video recordings, I observed 53 avian visits, including 35 feedings. The total visit length (from time of first appearance within the screen to time of disappearance from view) averaged 45 ± SEM 10 seconds, with a range from 1 second to nearly 28 minutes. Visits were most frequent between 0801 and 0900, followed by 1001 to 1100, and the most frequent feeding start time was between 0801 and 0900, followed by 0901 to 1000 (Fig. 2). From the 35 observed feedings, the average length of feeding time was 31.4 ± SEM 4.9 seconds, with a range of 1 second to 3 minutes. I defined feeding time as the time between the start and end of feeding actions, with greater than one minute between feeding motions constituting a separate event. On average, birds ate 5.3 ± SEM 0.6 fruits per feeding event (range: 1 to 14 fruits). Experimental bunch type did not affect the number of fruits eaten per visit (F2,32=0.524, P=0.597). Birds usually perched while
feeding (30 observations), although some individuals sallied and grabbed the fruit from the air (5 observations). I observed only two birds defecating, and thus potentially dispersing, while perched within view (i.e. near the fruit bunch). A wood thrush who perched for almost 28 minutes defecated once during that time, and a clay colored robin who stayed 7 minutes defecated three times.

Nine different bird species were observed eating fruit on the video recordings (Table 3). The larger bird species, such as clay colored robins (*Turdus grayi*, Turdidae), gray catbirds (*Dumetella carolinensis*, Mimidae), and buff throated saltators (*Saltator maximus*, Emberizidae), tended to perch and to eat more fruit per visit than smaller birds, such as the white-collared manakins (*Manacus candei*, Pipridae). All of these bird species are generalists, although manakins are largely frugivorous. Most species were residents, with two notable exceptions; gray catbirds and wood thrushes are winter migrants. An additional five species of birds were observed eating *Ardisia* not on video: red-capped manakins (*Pipra mentalis*, Pipridae; *Ardisia* seed found in defecation sample), golden-hooded tanagers (*Tangara larvata*, Thraupidae), dusky-faced tanagers (*Mitrospingus cassinii*, Thraupidae), blue gray tanagers (*Thraupis episcopus*, Thraupidae), and ochre-bellied flycatchers (*Mionectes oleaginous*, Tyrannidae).

**Discussion**

The highest fruit removal rates were from the 2R bunches (Table 2, Fig. 1), which had the most ripe fruits, suggesting that birds cued in on the ripe red color as well as the largest bunches. On average, birds removed the same number of fruits per visit from the three experimental bunch types; thus the higher overall removal rates from 2R bunches.
must have been due to more avian visits. In contrast to the preripening fruit flag hypothesis, there was no significant difference in fruit removals from R and R/U bunches, which had the same number of ripe fruits but differed in the presence or absence of unripe fruit. This suggested that (1) birds were not visually attracted by the colorful unripe fruit, and/or (2) the ripe fruit quantity did not exceed some hypothetical threshold of conspicuousness or profitability. Comparison of R/U and 2R, which had the same number of total fruit but different number of ripe fruit, revealed that birds preferred more ripe fruit. Comparison of R and 2R, which had different numbers of ripe fruit, also showed that birds were strongly attracted to more ripe fruits.

These results refute the preripening fruit flag hypothesis but support predictions based on optimal foraging theory (Stephens and Krebs 1986). Perhaps there was a threshold number of ripe fruits somewhere between 20 and 40 ripe fruits which signaled profitability and thus attracted the birds. An alternative explanation for the presence of sequential ripening with its corresponding fruit color change is physiological plant constraint of ripening all fruit at once. That is, if a plant has limited resources, at any given time it may only be able to ripen a few fruits at once. Another alternative is that differences in flowering or pollination phenology result in different fruit development times. Flowers opening in sequence or pollination at different times would lead to staggered fruit maturity. Finally unripe fruit color may actually serve as warning coloration, for example of repellent chemicals, to deter birds from taking unripe fruits (Janzen 1983). Some ripe fruits are known to have secondary metabolites that deter inappropriate dispersers (Cipollini and Levey 1997). Obviously it is most beneficial for the plant to have dispersal only of ripe fruits with fully developed seeds.
Fruit removal activity was highly variable depending on block location (Table 2). Indeed, some blocks rarely had any removals, while others had activity each time. There was no significant effect of tree location, indicating that my choice of locations was fairly standard within a block. Day was also not important; however, time of day was important, though it was not included in the ANOVA model. Birds fed the most in the morning period, and gradually less throughout the day (Fig. 1). Observation by video analysis suggested that feeding was greatest between eight and nine in the morning (Fig. 2).

Fourteen bird species in seven different families were observed eating *Ardisia* fruits. This immediately suggested that *Ardisia*’s fruit strategy is not directed at one particular bird species, especially because these were generalist feeders. Almost all bird species were residents, though the two migrant species were observed eating much fruit.

In a study similar to this one, Willson and Melampy (1983) found that bicolored fruit displays of *Prunus serotina* (black cherry) increased removal rates, but only in forest gaps versus forest interior. They suggest that bicolored displays may be more conspicuous to birds in a direct sense or by facilitating formation of a search image. My results of the opposite pattern, that multicolored fruit displays did not increase removal rates, could be for several reasons. It is unlikely the difference is because of light levels because my experimental bunches were placed within one meter of trails in secondary forests, which are comparable to gaps in light levels. It is possible that the different bird species involved have different foraging strategies. However, Willson and Melampy report that Mimids and thrushes were likely the birds feeding on their experimental fruit bunches. Surprisingly, the two migrants I observed in my study, gray catbirds and wood
thrushes, are also found in Illinois where their study was conducted. Finally, the different color schemes involved inherently attracted birds differentially. In their case, they used bicolored displays of immature red fruits and ripe black fruits. In my study, I used immature white and pink fruits and ripe red fruits. It is interesting to note that in both studies, the fruit bunches with red fruits were the most attractive. Red plant parts are often associated with bird use (Raven 1972). Perhaps the birds' detection of red color outweighed the factor of whether or not the displays were multicolored.

One final comparison of my study with that of Willson and Melampy (1983) is the removal rates in their temperate system versus my tropical one. They offered half as much fruit per display as I did and monitored the bunches for five consecutive days. From the data presented (only sets of data with some non-zero entries) of diurnal removals in forest gaps, their overall removal rate was 28.1% after five days. In contrast, for blocks with some non-zero entries, I had an overall removal rate 39.5% after a single day (in which I revisited bunches every four hours). This suggests that frugivory pressure is stronger in the tropical system. In fact, it may be that fruits are likely to be dispersed regardless of display, especially in the dry season when there is limited fruit availability (Levey 1988). Selective pressures on fruit traits may be stronger in temperate systems, but the fate of the dispersed seeds in both studies was unknown. It still may be more important in the tropics to disperse seeds to light gaps for germination to occur.

Overall, the results suggested that birds were not preferentially attracted to mixed fruit bunches with colorful unripe fruit. Fruit colors may be a compromise between conflicting selective pressures in attracting appropriate seed dispersers and avoiding inappropriate dispersers, seed predators, or fruit parasites (Wheelwright and Janson
1985). Despite these compromises, however, fruit color certainly plays a role in the attracting potential seed dispersers. In this study, birds located and ate fruits from bunches with the most ripe fruit.
Literature Cited


Willson, M.F. and J.N. Thompson. 1982. Phenology and ecology of color in bird-dispersed fruits, or why some fruits are red when they are "green". Canadian Journal of Botany 60: 701-713.


**Figure legends**

Fig. 1. The average cumulative number of ripe fruits removed over time from the three experimental fruit bunch types.

Fig. 2. Frequency histogram showing the number of observed visits and feeding events beginning during hourly intervals.
Table 1. Design of field experiments. (a) Number of fruits of each color in experimental fruit bunch treatments. (b) Sequence of treatments assigned to the three trees in each of the twelve blocks.

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<td>pink</td>
<td>red</td>
<td></td>
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<tr>
<td>R/U</td>
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b) Block design

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<td>R/U</td>
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<tr>
<td>2 (days 4-6)</td>
<td>R/U</td>
<td>2R</td>
<td>R</td>
</tr>
<tr>
<td>3 (days 7-9)</td>
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<td>R/U</td>
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Table 2. ANOVA table showing effect of bunch type, block, time period nested within block, and tree within block on the number of fruits eaten. Significant effects in bold type.

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<td>46</td>
<td>4191.426</td>
<td>91.118</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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Table 3. Bird species in order of decreasing body size and feeding mode observed on video recordings at experimental fruit bunches.

<table>
<thead>
<tr>
<th>Bird species</th>
<th>Feeding mode</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Turdus grayi</em> (Turdidae; clay colored robin)</td>
<td>perch</td>
</tr>
<tr>
<td><em>Dumetella carolinensis</em> (Mimidae; gray catbird)</td>
<td>perch</td>
</tr>
<tr>
<td><em>Saltator maximus</em> (Emberizidae; buff throated saltator)</td>
<td>perch</td>
</tr>
<tr>
<td><em>Hylocichla mustelina</em> (Turdidae; wood thrush)</td>
<td>perch</td>
</tr>
<tr>
<td><em>Habia fuscicauda</em> (Thraupidae; red throated ant tanager)</td>
<td>perch, sally</td>
</tr>
<tr>
<td><em>Myiarchus tuberculifer</em> (Tyrrannidae; dusky capped flycatcher)</td>
<td>perch, sally</td>
</tr>
<tr>
<td><em>Ramphocelus passerinii</em> (Thraupidae; scarlet rumped tanager)</td>
<td>perch</td>
</tr>
<tr>
<td><em>Pachyramphus cinnamomeus</em> (Tityridae; cinnamon becard)</td>
<td>perch</td>
</tr>
<tr>
<td><em>Manacus candei</em> (Pipridae; white collared manakin)</td>
<td>sally</td>
</tr>
</tbody>
</table>
Fig. 2

![Bar chart showing visit frequencies and feeding times per hour interval](image)

- **Visit**
- **Feeding**

**Start time of visit (per hour interval)**

- 6:01
- 7:01
- 8:01
- 9:01
- 10:01
- 11:01
- 12:01
- 13:01
- 14:01

**Frequency**

- 0
- 4
- 8
- 12
- 16