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Avian selection of the color-dimorphic fruits of salmonberry, *Rubus spectabilis*: a field experiment

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Although the mutualism between frugivorous animals and the fruiting plants whose seeds they disperse has been noted for over a century, it remains unclear whether animal selection has had any part in the evolution of fruit characteristics. We conducted field experiments using the color-dimorphic fruits of salmonberry (*Rubus spectabilis*) to determine whether free-ranging birds choose fruits on the basis of color, and if so, whether these patterns indicated the potential for birds to exert evolutionarily significant selective pressure on this fruit trait. Birds consistently selected red over orange fruits in experimental displays in the field despite wide geographic variation in fruit-color frequencies, fruit-crop densities, and numbers and species composition of avian frugivores in Oregon and Alaska. This is the first field study demonstrating significant and consistent fruit-trait selection by birds at a scale relevant to coevolutionary processes. These results indicate that forces other than animal selective pressure are also shaping the occurrence of fruit color traits in bird-dispersed fruiting plants.

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Many plants produce fleshy fruits. Many animals include these fruits in their diets, and to varying degrees, disperse the seeds found within them. Naturalists and ecologists have long speculated on the potential for coevolutionary pressures to shape this relationship (Darwin 1859, Ridley 1930, Snow 1971, McKey 1975, and many others). A great deal of research has been carried out in the past few decades exploring the extent of the mutualism.

Much of the work has focused on examining plant and animal species for traits that might be adaptive for frugivory and seed dispersal. Fruit type (Janson 1983), color (Turcek 1963, Janson 1983, Wheelwright and Janson 1985, Willson and Whelan 1990, and many others), size (Wheelwright 1985, Knight and Sigfried 1983, McPherson 1988), shape (Herrera 1992a), and nutrient content (Johnson et al. 1985, Whelan and Willson 1994) have all been studied from this perspective. However, fruit characteristics are often interrelated, making it difficult to examine any one trait for possible animal selection while holding other traits constant. Further, fruit characteristics may be the results of entirely unrelated processes, such as phylogenetic history (Herrera 1992a, b, Fischer and Chapman 1993, Jordano 1993). Animal selection of fruits is also influenced by factors unrelated to genetics, such as the background abundance of fruits from different species of plants (e.g. Denslow 1987, Jordano 1987, Sargent 1990). This complexity makes it even more difficult to directly assess adaptive relationships between fruits and frugivorous animals.

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Of all the fruit traits that may be the result of animal selective pressure, color has received most of the attention: it is a conspicuous trait, easy to identify and categorize, and lends itself to both broad-scale comparisons and to fine-scale experiments. A general pattern for regional floras to produce fruits that are red, black, or blue in color, or for birds to disproportionately consume fruits of these colors, has been noted for a number of regional plant and bird communities. These include plant communities in Europe (Turcek 1963), Peru (Janson 1983), Costa Rica (Wheelwright and Janson 1985), Gabon (Gautier-Hion et al. 1985), southern Africa (Knight and Sigfried 1983), and Australia and New Zealand (Willson et al. 1989). It is tempting to conclude that animal selection is the major cause behind these consistent trends in fruit color, but many other forces are also likely to be responsible (Willson and Whelan 1990).

For example, the biogeographic or phylogenetic history of the plants may constrain the evolution of the colors of fruits among related species (Willson and Whelan 1990, Herrera 1992a, b, Fischer and Chapman 1993, Jordano 1993). Color may play a physiological role in fruit development, as green fruits apparently retain the ability to photosynthesize (Cipollini and Levey 1991); alternatively, color may aid fruit development by defending the fruit from attack by insects (Willson and Thompson 1982). Colors may also be constrained by the physiological costs to the parent plant associated with pigment production (Willson and Whelan 1990). In the face of so many alternative possibilities, the only way to assess whether adaptation to frugivores is at least partially responsible for existing fruit characteristics is to determine whether frugivores demonstrate the ability to discriminate between and consistently select certain fruit traits over others.

Discrimination among palatable fruits based on color variation has been shown by birds in aviaries. Experiments using both real and artificial fruits have demonstrated that when other factors such as fruit size, seed size, and nutrient content are held constant, individual birds do demonstrate preference for some colors over others: in general, red and black are preferred over yellow and green (McPherson 1988, Murray et al. 1993, Willson and Comet 1993, Willson 1994, Puckey et al. 1996). Consumer species tested included American robins (*Turdus migratorius*, Willson 1994), cedar waxwings (*Bombycilla cedrorum*, McPherson 1988), silvereyes (*Zosterops lateralis*, Puckey et al. 1996), northwestern crows (*Corvus caurinus*, Willson and Comet 1993), gray catbirds (*Dumetella carolinensis*, Whelan and Willson 1994), and Swainson's and hermit thrushes (*Catharus ustulatus* and *C. guttatus*, Traveset and Willson in press). However, individuals varied greatly in the colors that they preferred, and in the strengths of those preferences (Murray et al. 1993, Willson and Comet 1993, Willson 1994, Traveset and Willson in press). In some experiments, color preferences were either weak (Willson et al. 1990), or disappeared over time (McPherson 1988). The few field experiments designed to determine whether wild populations of birds exhibit color selection have been conducted on a small spatial scale, and have not found clear evidence that birds selected fruits on the basis of color (Willson 1983, Willson and O'Dowd 1989).

These mixed results suggest that birds have very little to do with the constrained patterns of fruit color variation noted in the various regional floras. However, a major difficulty in clarifying ecological and evolutionary relationships lies in determining the appropriate scale to use during experimentation. Observed evolutionary processes and patterns are the sum of the individuals' actions at the level of the population (Thompson 1994). Accordingly, investigations into the potential for frugivore choice to influence fruit characteristics should be carried out at the scale of the population. Such experiments will be more likely to detect the existence of dominant patterns of selection that emerge from variation at the scale of individual organisms.

In this study, we expanded the scale of investigation beyond aviary experiments to field experiments to test whether wild bird populations demonstrate fruit color selection when making foraging decisions. We created small patches of fruit made up of the two color morphs of salmonberry (*Rubus spectabilis* Pursh, Rosaceae) and embedded them in naturally occurring salmonberry thickets. These manipulations allowed us to examine color choice of avian frugivores against a variable background of fruit-color frequencies at both local and regional scales. If birds are selective agents constraining the evolution of fruit color, they should demonstrate consistent color selection regardless of background frequencies of the fruits. If birds' choices are merely a reflection of their previous foraging experiences, then fruit removal should occur proportionately to the background color frequencies. Finally, if birds do not use color as a selective criterion, fruits should be removed from the display patches in proportion to their abundance.

Methods

Study sites and species

Rubus spectabilis is a cane-producing shrub that extends along the eastern Pacific coast from central California to south-central Alaska, and produces color-dimorphic fruits throughout its range. Color-polymorphic fruits in *R. spectabilis* and other plant species are very similar to each other in size and nutrient content (Willson 1983, Willson and O'Dowd 1989, Traveset and Willson in press). Many North American plant species produce color-polymorphic fruits (Willson 1986), but *R. spectabilis* is unusual in that not only do both fruit-color morphs usually occur together at a site, but even the rarer morph is typically quite common. These traits result in adequate supplies of fruits of both colors for field experiments.

Although many mammals eat *R. spectabilis* fruits, particularly bears (*Ursus americanus* and *U. arctos*), in our study sites the fruits appeared to be removed primarily by birds, judging from both direct observations and the lack of mammal sign (i.e., scat with salmonberry seeds). Bear consumption in particular is marked by widespread damage to the plants, and this was evident in only one site in Alaska, occurring after many of the salmonberry fruits had already ripened and had been removed by birds.

We tested for fruit-color selection by birds in the Waldport District of the Siuslaw National Forest in the Coast Range of Oregon, and in Southeast Alaska near Juneau. In each state, we located eight sites with abundant salmonberry; all were easily accessible by roads and trails. Sites were distributed over Oregon and Alaska in areas 15 km and 50 km long, respectively. Surveys of the fruit dimorphism in the Siuslaw National Forest from a pilot study conducted the previous year indicated that morph frequencies were similar throughout the region, whereas in Southeast Alaska, they varied tremendously among sites. At the time of the experiments, no other fruit species were ripe in the study area in Oregon. Ripe blueberries (*Vaccinium* spp.) dominated one site in Alaska; in others, red elderberry shrubs (*Sambucus racemosa*), devil's club (*Opoplanax horridum*), and Swedish dwarf cornel (*Cornus suecica*) had also produced ripe fruit by the end of the experimental period. We conducted fieldwork in Oregon 25 May–22 June and in Alaska 5–31 July, 1996; full site descriptions and dates are given elsewhere (Gervais 1996). Experiments were run concurrently within states as much as logistically possible; in all cases, there was at least some temporal overlap.

Fruit-color selection experiments

We designed paired experimental displays to test for avian frugivore color selection in three sites per state. These were selected from different watersheds at least 5 km apart to increase independence of the frugivorous bird communities among sites.

For the experiments in each site, we cut canes of *R. spectabilis* bearing ripe fruits and placed them in 40-cm lengths of 7.5 cm diameter plastic ABS pipe pounded into the ground. The pipes were lined with paper cups and plastic bags to hold water, and we placed the two pipes within 10–20 cm of each other. We presented the colors separately, one color per pipe, and determined the positions randomly. Each display station contained twelve fruits of each color morph. Fruits were taken from more than one microsite to represent phenotypic variability in fruit characteristics (Willson and Whelan 1993).

We set up 10 display stations every 200 m on a 2-km transect of random origin at each site. The transects were placed in extensive thickets of salmonberry so that all display stations had at least some naturally occurring *R. spectabilis* within a few meters. We placed display stations at the edges of clearings or under overstory vegetation to avoid rapid deterioration of the display fruits. Canes were cut for the displays away from the display site until after the vegetation had been measured to avoid biasing the measurements. This was particularly important in sites where one color morph was rare, since removing canes of that morph might substantially bias sampling results.

We visited each display station daily and counted the number of remaining fruits until most displays had had all the fruits removed. Any canes with discolored or moldy fruits were replaced with fresh canes bearing the same number of fruits so that visiting birds would not be biased in their selection by any visible fruit deterioration. Canes whose fruits had apparently fallen from the displays were also replaced, as were those whose fruits were eaten by rodents. We identified fallen fruits as entire fruits lying directly beneath the display; rodent removal was identified by the bits of seed husk and pulp that appeared beneath the display. Birds either removed the whole fruit or more rarely, pecked off sections, leaving intact seeds surrounded by pulp. Such fruits were considered removed. Fewer than 5% of all fruits used in the displays were abscised or eaten by rodents.

For each display station, we determined the median number of days between first removal of any fruit and the depletion of all fruits of one of the color morphs. Median time to removal was used due to the great variation in removal patterns among stations. We then determined the number of fruits of each morph that had been removed by the median day. Since the fates of red and orange fruits at each display are not likely to be independent of each other, we calculated the differences in the number of fruits removed by subtracting the number of orange fruits removed from the number of red fruits removed. Two display stations at one site in Oregon were never visited by frugivorous birds, and a bear repeatedly destroyed two stations at one site in Alaska. These display stations were removed from this analysis.

We performed a nested analysis of variance (ANOVA) on the differences, with site nested within state. Since neither state nor site had significant effects ($F_{1,4} = 2.19$, $P = 0.21$; $F_{4,50} = 0.14$, $P = 0.97$ for state and site within state, respectively), we compared differences across all sites using a paired t-test to examine the null hypothesis that there was no consistent color selection. We used

SAS (SAS 1989) for all statistical analyses, with the exception of the loglinear modeling, which was done with NCSS (Hintze 1990).

We tested for differences in the rates of fruit removal among sites and between states by comparing the numbers of fruits removed by the median date for the two color morphs separately and combined. In each case, a nested ANOVA was used, with site nested within state and both factors considered fixed. Sites were considered fixed in this case because a very specific subsample of the total sites examined was chosen for the experiments based on requirements of size, distance from each other, and presence of fruiting plants (Bennington and Thayne 1994). When all sites were considered together, as when fruit crop attributes were compared, the effect of site was considered to be random since the initial selection of sites for the study was based solely on the presence of *R. spectabilis* and accessibility by roads or trails.

Fruit-color frequency, density, size, and nutrient content

We estimated fruit-color frequencies within naturally occurring salmonberry populations at our study sites to determine if background effects were contributing to avian fruit selection, and we examined a number of attributes of the naturally occurring salmonberry in our study sites. We estimated the color-morph frequencies in each of the 16 sites using a systematic sampling design, measuring 1-m^2 quadrats every 5 m on transects 50 m long. In large patches such as clearcuts, we randomly placed 10 to 15 transects perpendicular to the edge or to a central road. Linear patches growing along trails or streams were measured with 10 transects placed end to end from a random start; in long patches, the transects were alternated with 50-m gaps. Within the quadrats, we recorded the per cent cover of *R. spectabilis*, the numbers of fruits of each color morph, and the phenological state of all fruits as either green, ripe, or removed/rotted.

The proportion of red fruits in each population is the total number of red fruits divided by the sum of both red and orange fruits per site. Unidentifiable fruits were excluded; these fruits were green, missing, or rotten, and lacked identifiable fruits on the same cane. The proportions of red fruit per site were arcsine-square-root transformed (Zar 1984), then compared between states using a two-sample *t*-test. We compared the proportions of quadrats per site containing fruits using a chi-square test to test for differences among sites in the proportion of *R. spectabilis* producing fruit. Ripening synchrony between color morphs, sites, and states was compared using loglinear analysis (Fienberg 1977, Knoke and Burke 1980, Hintze 1990). Finally, we compared densities of fruits per quadrat between sites and states using nested ANOVA tests. Since states were chosen to represent the extremes of *R. spectabilis* distribution, we considered the state effect to be fixed, whereas the factor of sites within states was considered to be random as discussed above (Zar 1984, Bennington and Thayne 1994). We compared densities of fruits using all quadrats that contained *R. spectabilis* canes. After log-square-root transformation, the data met the assumption of equality of variances. Since sites differed in the number of quadrats sampled, F statistics were calculated using the type III sums of squares, as they are believed to be most reliable for unbalanced designs (Shaw and Mitchell-Olds 1993).

To ensure that consistent differences in fruit size were not responsible for fruit selection, we compared fruit sizes between the two color morphs, collecting 19 fruits of each morph from two sites in Oregon, and 29 fruits of each morph from two sites in Alaska. Fruit lengths and widths were measured to the nearest mm and compared using a two-factor ANOVA. Both dimensions were measured because salmonberry fruits can be quite variable in shape. Since fruit dimensions were highly correlated ($r = 0.91$), we performed a principal components analysis on the log-transformed data; the first factor accounted for 94.6% of the variance. We then tested for differences among factor scores using nested ANOVA. Site was nested within state, and state and color were crossed. We considered all effects fixed, as we collected the fruits from sites where we had placed removal displays.

We collected fruits of each morph at the three removal sites in Oregon, removed the seeds, and submitted the combined sample of each morph for analysis of nitrogen, water, lipid, and overall sugar content. Samples of fruits from the Juneau area had been tested previously (Traveset and Willson in press). Since the cost of the laboratory analyses prevented us from submitting more than one sample per color morph per state, no statistical comparisons were possible.

Surveys of avian frugivores

We estimated the composition and relative abundance of the avian frugivore community using point count surveys (Hutto et al. 1986) centered on the removal display stations. Each survey consisted of an 8-min count period during which we recorded all birds detected within 0–50 and 50 + m radius bands. After each 8-min survey we played recorded songs of the four thrush species likely to occur in these sites: American robin, Swainson's thrush, hermit thrush, and varied thrush (*Ixoreus naevius*). These trials consisted of 1 min of song playback at constant volume, followed by 1 min of silence while we looked for birds and listened for vocal responses. All surveys were conducted between 05:00 and 10:00, and all removal display sta-

Table 1. State, sample size, median times to removal of all fruits in experimental displays (MTR), and fruits removed of each color morph for each site. Values are means ± 1 standard error. The number of experimental fruit removal displays that were visited by birds is indicated by *n*. The location number is listed under site.

State	Site	*n*	MTR (days)	Fruits removed		
				Red fruits	Orange fruits	Total fruits
OR	2	10	3.6 ± 0.9	4.6 ± 1.3	2.1 ± 0.6	6.7 ± 1.2
	4	8	4.2 ± 0.7	5.8 ± 1.5	4.0 ± 0.8	9.8 ± 1.9
	6	10	1.9 ± 0.5	7.7 ± 0.8	5.5 ± 1.1	13.2 ± 1.5
Overall		28	3.1 ± 0.4	6.0 ± 0.7	3.9 ± 0.6	9.9 ± 1.0
AK	1	8	2.0 ± 0.6	5.5 ± 1.2	3.5 ± 0.9	9.0 ± 1.9
	2	10	3.2 ± 0.6	6.2 ± 1.2	5.2 ± 1.0	11.4 ± 2.2
	5	10	4.0 ± 0.8	6.5 ± 1.1	4.7 ± 1.2	11.2 ± 2.2
Overall		28	3.1 ± 0.4	6.1 ± 0.6	4.5 ± 0.6	10.6 ± 1.1

tions at a site were surveyed the same morning with a few exceptions related to weather and bear activity. Each site was surveyed three times while fruit selection experiments were in progress. We varied the order of visits to display stations within a site to avoid systematic time biases in the surveys.

We summed the numbers of thrushes detected per visit within 50 m of each display station and the number of thrushes detected during the song playback period, and used the greater of these two counts for analyses. Although we did not include cedar waxwings (*Bombycilla cedrorum*) or bohemian waxwings (*B. garrulus*) in the song playbacks, we added any waxwings recorded to the total, as these species are highly frugivorous (Ehrlich et al. 1988, Levey and Grajal 1991). Although we observed other bird species such as spotted towhees (*Pipilo erythrophthalmus*), white-crowned sparrows (*Zonotrichia leucophrys*) and fox sparrows (*Passerella iliaca*) eating salmonberry, we did not include them in the analysis because of their generally much lower levels of frugivory, and their relatively low detection frequency. In addition, sparrows have much less predictable effects on seed survival, whereas seeds eaten by thrushes show high rates of germination success (Barnea et al. 1990, Izhaki and Safriel 1990, Traveset and Willson in press). The total numbers of thrushes and waxwings detected were compared using a nested ANOVA, with state and site within state considered fixed effects, and station within site and state considered a random effect. Site was a fixed effect in this case because only those sites with removal displays were surveyed for frugivorous birds.

Relationships between numbers of birds, color-morph dominance, and fruit selection

We used analysis of covariance (ANCOVA) to examine relationships between the number of thrushes and waxwings detected at a removal display station and the numbers of fruits removed from the displays. We performed ANCOVAs on red and orange fruits separately and combined, using the numbers of thrushes and waxwings detected as the covariate. We also performed correlation analyses to examine possible relationships between the number of thrushes and waxwings detected, the density of fruits per quadrat, and the average median fruit removal date for each of the six sites for which all of these data were recorded.

Results

Fruit-color selection experiments

Birds selected more red fruits than orange fruits, regardless of site or state (Table 1). The mean difference in fruits removed per display between the two color morphs was 1.84 fruits, which, at our sample size, was statistically significant ($t = 3.78$, $P < 0.01$, $n = 56$).

Birds removed fruits at similar rates among sites. There was no difference in the numbers of fruits eaten by the median date between states or among sites within states (Table 2). Median times to depletion also did not differ significantly between states ($F_{1,4} = 0.03$, $P = 0.86$), although there was some evidence that they did vary among sites within states ($F_{4,50} = 2.37$, $P = 0.07$).

Table 2. Nested ANOVA comparing numbers of fruits eaten by the median date between sites. The effect of SITE was nested within STATE, and both effects were fixed. Mean values for each variable are given in Table 1.

Source of variation	df	MS	*F*	*P* > *F*
I. Red fruits				
STATE	1	0.0154	0.00	0.97
SITE (STATE)	4	12.8558	2.01	0.41
Error	50	12.69		
II. Orange fruits				
STATE	1	4.9846	0.28	0.63
SITE (STATE)	4	17.8232	2.01	0.11
Error	50	8.8520		
III. Total fruits				
STATE	1	5.5538	0.09	0.78
SITE (STATE)	4	59.3290	2.07	0.10
Error	50	28.6335		

Table 3. Proportions of sampled quadrats that contained fruiting *R. spectabilis* canes, and mean fruit densities per m^2-quadrat ± 1 SE. Asterisks indicate sites used for fruit removal experiments. Means by state are listed at the bottom.

Oregon				Alaska			
Site	n	Proportion	Density	Site	n	Proportion	Density
1	85	0.46	2.5 ± 0.5	1*	200	0.67	5.2 ± 0.5
2*	91	0.66	6.8 ± 1.0	2*	93	0.68	8.0 ± 1.1
3	74	0.55	4.3 ± 0.7	3	91	0.56	3.6 ± 0.7
4*	128	0.66	5.8 ± 0.7	4	79	0.54	4.6 ± 0.9
5	49	0.55	2.7 ± 0.5	5*	95	0.40	1.9 ± 0.5
6*	79	0.52	4.6 ± 0.9	6	90	0.78	8.1 ± 0.9
7	92	0.53	3.7 ± 0.5	7	72	0.88	24.1 ± 2.8
8	83	0.64	5.6 ± 0.8	8	95	0.76	8.1 ± 1.0
OR	681	0.58	4.7 ± 0.3	AK	815	0.65	6.0 ± 0.4

Table 4. Phenological comparisons using proportions of ripe fruits of each color morph per site and state. Sample sizes are the number of fruits counted of each color morph and are given in parentheses. Means are listed for each state at the bottom. Asterisks indicate sites used for removal experiments.

OR	Red	Orange	AK	Red	Orange
1	0.30 (23)	0.56 (171)	1*	0.26 (703)	0.25 (287)
2*	0.28 (131)	0.26 (467)	2*	0.39 (381)	0.51 (372)
3	0.39 (61)	0.30 (251)	3	0.31 (297)	0.32 (31)
4*	0.41 (37)	0.39 (689)	4	0.20 (224)	0.26 (129)
5	0.23 (13)	0.24 (95)	5*	0.23 (113)	0.31 (51)
6*	0.16 (104)	0.27 (256)	6	0.23 (571)	0.27 (153)
7	0.34 (68)	0.49 (257)	7	0.26 (1356)	0.14 (264)
8	0.50 (4)	0.37 (454)	8	0.32 (625)	0.44 (147)
OR	0.29 (441)	0.36 (2640)	AK	0.28 (4270)	0.32 (1434)

Fruit-color frequency, density, size, and nutrient content

Alaska consistently had a much greater proportion of red fruits than Oregon ($\bar{x} = 0.73$, SE = 0.05, and $\bar{x} = 0.15$, SE = 0.03 for Alaska and Oregon, respectively; $t = 8.69$, $P < 0.01$, $n = 8$). Across all sites sampled, the proportion of unidentifiable fruits per site averaged 0.04 (SE = 0.01, $n = 16$), and the results of comparing proportions did not change when the unidentifiable fruits were added to either color category.

The proportion of quadrats with fruiting canes and the density of fruits per square meter also varied from site to site. A greater proportion of quadrats in Alaska contained fruiting *R. spectabilis* canes ($\bar{x} = 0.66$, SE = 0.05, $n = 815$) than in Oregon ($\bar{x} = 0.57$, SE = 0.01, $n = 681$; $\chi^2 = 8.91$, $P < 0.01$). Sites also varied significantly in the proportion of quadrats containing fruiting stems ($\chi^2 = 81.0$, $P < 0.01$, Table 3). States did not differ in the mean densities of fruits per quadrat ($F_{1,14} = 1.86$, $P = 0.19$) but there was significant among-site variation ($F_{14,1480} = 10.45$, $P < 0.01$, Table 4). Sites with the highest densities of fruits also had the greatest proportions of quadrats with fruiting canes ($r = 0.82$, $P < 0.01$, $n = 16$).

The consistent selection of red fruits was not based on phenology, or which color morph ripened first; there was no difference between the proportions of ripe fruits of each of the color morphs within sites ($t = 1.35$, $P = 0.20$, $n = 16$, Table 4). The only loglinear model that gave an adequate statistical fit to the phenological data included the interaction of all model factors. In other words, ripening phenology varied with fruit color, state, and site; the two morphs were not consistently different from each other between states or among sites. Fruit selection, therefore, was not based on ripening phenology.

Fruit selection was also not based on fruit size. Size did not differ between the two color morphs (Table 5), although the overall size of fruits varied significantly among both sites and states. Fruits in Oregon tended to be larger than those in Alaska (Table 6).

Table 5. Crossed, nested ANOVA testing for differences in fruit sizes between color morphs, states, and sites within states. COLOR was crossed and SITE was nested within STATE. All factors were considered fixed. The data used for the analysis were the factor scores generated from the first eigenvector of a PCA conducted on the log-transformed values of fruit length and width.

Source of variation	df	MS	F	$P > F$
COLOR	1	0.7730	2.04	0.16
STATE	1	110.2668	24.10	0.04
SITE (STATE)	2	4.5760	12.06	0.00
COLOR × STATE	1	0.9811	0.21	0.11
COLOR × SITE (STATE)	2	0.2148	0.57	0.57

Table 6. Summary of fruit sizes for each color morph by site and state. Values are the means in mm ± 1 standard error: sample sizes are the number of fruits measured and are given in parentheses. The overall mean site values per state ± 1 standard error are also given.

State	Site	Red fruits		Orange fruits	
		Length	Width	Length	Width
OR	2	29.3 ± 1.3 (19)	31.5 ± 1.2 (19)	31.0 ± 0.8 (19)	32.3 ± 0.8 (19)
	6	23.3 ± 1.2 (19)	26.8 ± 1.4 (19)	26.8 ± 0.9 (19)	27.5 ± 1.2 (19)
Overall		26.3 ± 1.0 (38)	29.2 ± 1.0 (38)	28.9 ± 0.7 (38)	29.9 ± 0.9 (38)
AK	1	18.6 ± 0.5 (29)	18.9 ± 0.5 (29)	18.8 ± 0.7 (29)	19.8 ± 0.6 (29)
	2	19.0 ± 0.6 (29)	19.4 ± 0.5 (29)	17.4 ± 0.5 (29)	19.8 ± 0.5 (29)
Overall		18.8 ± 0.4 (58)	19.2 ± 0.4 (58)	18.1 ± 0.4 (58)	19.8 ± 0.4 (58)

Table 7. Comparisons of nutrient content between red and orange morph fruits in Oregon and Alaska. All values are given as percentages. Percent water readings were taken at 65°C, and TNC is the total nonstructural carbohydrate content, or sugars.

	Oregon				Alaska			
	N	Lipid	TNC	H_2O	N	Lipid	TNC	H_2O
Orange	1.01	1.34	27.0	94.12	1.23	4	40.4	91
Red	1.00	1.04	30.4	94.55	1.11	4	39.0	99

Table 8. Mean numbers of thrushes and waxwings detected per 8-min survey at each site. Total numbers of thrushes and waxwings combined over all three surveys are also given. Values are means ± 1 standard error; $n = 10$ surveys in all cases. The mean of the total numbers detected per site by state are also listed ± 1 standard error ($n = 3$).

	State					
	OR			AK		
Site	2	4	6	1	2	5
Survey 1	1.7 ± 0.4	2.4 ± 0.4	1.7 ± 0.3	2.7 ± 0.5	2.8 ± 0.4	1.0 ± 0.3
Survey 2	1.3 ± 0.2	2.1 ± 0.4	1.7 ± 0.3	2.1 ± 0.6	3.2 ± 0.4	0.5 ± 0.3
Survey 3	1.2 ± 0.3	1.9 ± 0.7	1.7 ± 0.2	1.1 ± 0.4	2.2 ± 0.3	0.7 ± 0.3
Total	4.2 ± 0.4	6.4 ± 1.0	5.1 ± 0.4	5.9 ± 0.8	8.2 ± 0.6	2.2 ± 0.6
Overall		5.2 ± 0.6		5.4 ± 1.8		

Fruits of the two morphs varied somewhat in nutrient content between states, but much less so between morphs within a state (Table 7). Red fruits contained more water than orange fruits in Alaska, and red fruits contained slightly greater sugar content and less lipid content in Oregon than the fruits of the orange morph.

Surveys of avian frugivores

The numbers of thrushes and waxwings detected did not differ between states nor among removal display stations ($F_{1,4} = 0.01$, $P = 0.92$ and $F_{54,120} = 1.07$, $P = 0.38$ for state and station, respectively), but sites within states did show significant variation ($F_{4,54} = 11.2$, $P < 0.01$, Table 8).

Relationships between numbers of birds, color-morph dominance, and fruit selection

There was no evidence of a relationship between the total numbers of fruit removed by the median date and the numbers of frugivorous birds (Table 9), and the numbers of thrushes and waxwings did not explain a significant amount of variance. The numbers of red fruits removed did not differ among sites or between

Table 9. ANCOVA of number of fruits removed per display station using the total number of thrushes detected at that station as a covariate. SITE was nested within STATE; both factors were fixed.

Source of variation	df	MS	F	$P > F$
I. Red fruits				
STATE	1	4.6043	0.25	0.64
SITE (STATE)	4	18.4713	1.44	0.23
BIRDS	1	33.8895	2.64	0.11
Error	51	12.8174		
II. Orange fruits				
STATE	1	12.5789	0.64	0.47
SITE (STATE)	4	19.7969	2.19	0.08
BIRDS	1	7.7587	0.86	0.36
Error	51	9.0283		
III. Total fruits				
STATE	1	32.4039	0.43	0.55
SITE (STATE)	4	74.6440	2.52	0.05
BIRDS	1	74.0791	2.5	0.12
Error	51	29.6019		

states, but there was weak evidence that the numbers of orange fruits removed differed among sites. There were no differences between states, however. There was no evidence that color-morph dominance influenced the numbers of fruits removed of each morph.

There were no significant correlations between the numbers of thrushes and waxwings detected per site and the median time to removal ($r = -0.24$, $P = 0.65$, $n = 6$), or between the fruit density and the median date of removal for each site ($r = -0.07$, $P = 0.90$, $n = 6$). The numbers of thrushes and waxwings per site, however, were correlated with the densities of fruits per square meter ($r = 0.81$, $P = 0.05$, $n = 6$).

Discussion

At the population scale, birds consistently selected red over orange fruits in the displays regardless of the locally occurring fruit-color frequencies or densities. To the best of our knowledge, this is the first study demonstrating frugivore selection of a fruit trait at a scale relevant to potential coevolutionary processes. Although we cannot conclude that patterns of fruit-color occurrence are the result of frugivore selection, we demonstrated the potential for avian frugivores to exert consistent selective pressure at both local and regional spatial scales. This result contrasts with the ambiguity of the combined results of aviary experiments carried out by a number of researchers (e.g., McPherson 1988, Willson et al. 1990, Willson and Comet 1993, Willson 1994). It is in general agreement with the work comparing fruit colors and apparent frugivore choice patterns among regional floras (Turcek 1963, Janson 1983, Knight and Sigfried 1983, Gautier-Hion et al. 1985, Wheelwright and Janson 1985, Willson et al. 1989), where red was a dominant color.

The consistent numbers of fruits and placement of the two color morphs adjacent to each other in the removal displays controlled for the effects of crop size and the possibility in natural populations that the different fruit-color morphs might not occupy the same microsite. Fruit crop size has been shown to influence fruit selection (Moore and Willson 1982, Davidar and Morton 1986, Denslow 1987, Jordano 1987, Bodmer 1990, Thebaud and Debussche 1992; but see French et al. 1992 and Laska and Stiles 1994). The conspecific neighborhoods surrounding the experimental removal displays were highly variable, ranging from canes with no fruits present to high densities of fruits, and color-morph frequencies that ranged from 5% to over 70% red. Despite the background variability, the neighborhood effects in this study had no apparent influence over color-morph selection. This also contrasts with previous work (Moore and Willson 1982, Denslow 1987, Sargent 1990, Sallabanks 1993, Willson and Whelan 1993). The fact that environmental factors beyond the control of the parent plants were insufficient to counter overall patterns of frugivore selection supports the argument that fruit color is a factor in fruit selection by birds, and that this selection is of potential evolutionary significance to fleshy-fruited plants.

Red fruits of *R. spectabilis* were selected consistently over the orange morph fruits. The consumer-recognition hypothesis may help explain why red fruits were chosen even when the fruits of this color morph were quite rare (Stephens and Krebs 1986). In this case, color selection may be specific to the type of color polymorphism found in *R. spectabilis*. Fruit-color polymorphisms can be divided into two general types: one where one of the colors is a variant form caused by a lack of pigment; and a second type, in which the colors represent gradients along a developmental pathway. *R. spectabilis* belongs in the latter category. Red salmonberry fruits undergo similar color changes developmentally as the orange fruits, except that they darken to red during the final ripening (our personal observation). An orange-colored fruit can therefore represent a ripe, ready-to-eat orange fruit, or a hard, unripe red fruit. For humans, it is often difficult to distinguish the two without resorting to examining the rest of the cane for ripe fruits, or handling the questionable fruits to determine hardness. Birds may have similar difficulty, and may choose to select the fruit color that is always ripe.

Color-morph frequency of *R. spectabilis* varied substantially between sites and among states. These variable fruit-color frequencies did not reflect frugivore choice at either a local or regional scale. This pattern highlights the limitations of selective forces on the evolution of fruit traits: clearly, seed disperser pressure is not the only factor. In the case of *R. spectabilis*, its reproductive strategy may dilute any frugivore selection. Salmonberry spreads very readily through rhizomes and is therefore able to persist almost indefinitely at a site without sexual reproduction (Tappeiner et al. 1991, Tappeiner and Zasada 1993, Zasada et al. 1994). Further, the geographic variation in color-morph dominance suggests that factors such as soils or climate may be acting on plant traits that are correlated with, but not related to, the fruit color morph: the colors may simply be by-products of selection acting on these correlated characters (Willson and Whelan 1990). For example, the various fruit-color morphs of *Rhagodia parabolica* produce seeds with differing dormancy periods before germination (Willson and O'Dowd 1989), and banana slug (*Ariolimax columbianus*) ingestion of *R. spectabilis* inhibited germination more strongly in the red than the orange morph seeds (Gervais et al. in press). Interestingly, bird and bear ingestion of salmonberry fruits did not produce a differential germination effect between color morphs (Traveset and Willson 1997), although ingested seeds showed enhanced germination over control seeds. Preliminary work with soils indicated that the two *R. spectabilis* fruit-color morphs may germinate at different rates depending on the soil type (Traveset and Willson in press). Germination behavior is very unlikely to be a consequence of fruit color. To the extent that this character correlation occurs, the ability of a plant species to respond to selective pressure on any one trait is considerably lessened, along with the potential for adaptive responses.

In conclusion, birds consistently selected the red color morph of *R. spectabilis* on both local and regional scales. The pattern of selection occurred despite differences in the numbers and species of frugivores present, and the very different background abundances and frequencies of the two color morphs. This result demonstrates that avian frugivores have the potential to apply evolutionarily significant pressure on the plants whose fruits they eat and whose seeds they disperse. However, the fact that the fruit-color morph distribution patterns were independent of frugivore preference suggests that many other factors are likely to play a role in plant responses. Finally, the relationship between the frugivore color selection detected in this study and the reproductive strategy of *R. spectabilis* remains uncertain.

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References

Barnea, A., Yom-Tov, Y. and Friedman, J. 1990. Differential germination of two closely related species of *Solanum* in response to bird ingestion. – Oikos 57: 222–228.

Bennington, C. C. and Thayne, W. V. 1994. Use and misuse of mixed model analysis of variance in ecological studies. – Ecology 75: 717–722.

Bodmer, R. E. 1990. Fruit patch size and frugivory in the lowland tapir (*Tapirus terrestris*). – J. Zool. 222: 121–128.

Cipollini, M. L. and Levey, D. J. 1991. Why some fruits are green when they are ripe: carbon balance in fleshy fruits. – Oecologia 88: 371–377.

Darwin, C. 1859. On the origin of species. – Murray, London.

Davidar, P. and Morton, E. S. 1986. The relationship between fruit crop sizes and fruit removal rate by birds. – Ecology 67: 262–265.

Denslow, J. S. 1987. Fruit removal from aggregated and isolated bushes of the red elderberry *Sambucus pubens*. – Can. J. Bot. 65: 1229–1235.

Ehrlich, P. R., Dobkin, D. S., and Wheye, D. 1988. The birder's handbook. – Simon & Schuster, New York.

Fienberg S. E. 1977. The analysis of cross-classified data. – MIT Press, Cambridge, MA.

Fischer, K. E. and Chapman, C. A. 1993. Frugivores and fruit syndromes: differences in patterns at the genus and species level. – Oikos 66: 472–482.

French, K., O'Dowd, D. J. and Lill, A. 1992. Fruit removal of *Coprosma quadrifida* (Rubiaceae) by birds in south-eastern Australia. – Aust. J. Ecol. 17: 35–42.

Gautier-Hion, A., Duplantier, J. M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Mougazi, A. and Thiollay, J.-M. 1985. Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. – Oecologia 65: 324–337.

Gervais, J. A. 1996. Fruit color polymorphism in salmonberry *Rubus spectabilis* Pursh (Rosaceae) and fruit selection by free-ranging birds. – Master's thesis, Humboldt State Univ., Arcata, CA.

Gervais, J. A., Traveset, A. and Willson, M. F. In press. The potential for seed dispersal by the banana slug (*Ariolimax columbianus*). – Am. Midl. Nat.

Herrera, C. M. 1992a. Interspecific variation in fruit shape: allometry, phylogeny, and adaptation to dispersal agents. – Ecology 73: 1832–1841.

Herrera, C. M. 1992b. Historical effects and sorting processes as explanations for contemporary ecological patterns: character syndromes in Mediterranean woody plants. – Am. Nat. 140: 421–446.

Hintze, J. L. 1990. Number cruncher statistical system ver 5.8: advanced tables. – Kaysville, UT.

Hutto, R. L., Pletschet, S. M. and Hendricks, P. 1986. A fixed-radius point count method for nonbreeding and breeding season use. – Auk 103: 593–602.

Izhaki, I. and Safriel, U. N. 1990. The effect of some Mediterranean scrubland frugivores upon germination patterns. – J. Ecol. 78: 56–65.

Janson, C. H. 1983. Adaptations of fruit morphology to dispersal agents in a neotropical forest. – Science 219: 187–189.

Johnson, R. A., Willson, M. F., Thompson, J. N. and Bertin, R. I. 1985. Nutritional values of wild fruits and consumption by migrant frugivorous birds. – Ecology 66: 819–827.

Jordano, P. 1987. Avian fruit removal: effects of fruit variation, crop size, and insect damage. – Ecology 68: 1711–1723.

Jordano, P. 1993. Geographical ecology and variation of plant-seed disperser interactions: southern Spanish junipers and frugivorous thrushes. – In: Fleming, T. H. and Estrada, A. (eds), Frugivory and seed dispersal: ecological and evolutionary aspects. Kluwer, Belgium.

Knight, R. S. and Sigfried, W. R. 1983. Inter-relationships between type, size and colour of fruits and dispersal in southern African trees. – Oecologia 56: 405–412.

Knoke, D. and Burke, P. J. 1980. Log-linear models. – Sage, London.

Laska, M. S. and Stiles, E. W. 1994. Effects of fruit crop size on intensity of fruit removal in *Viburnum prunifolium* (Caprifoliaceae). – Oikos 69: 199–202.

Levey, D. J. and Grajal, A. 1991. Evolutionary implications of fruit-processing limitations in cedar waxwings. – Am. Nat. 138: 171–189.

McKey, D. 1975. The ecology of coevolved seed dispersal systems. – In: Gilbert, L.E. and Raven, P. H. (eds), Coevolution of animals and plants. Univ. of Texas Press, Austin, TX.

McPherson, J. M. 1988. Preferences of cedar waxwings in the laboratory for fruit species, colour and size: a comparison with field observations. – Anim. Behav. 36: 961–969.

Moore, L. A. and Willson, M. F. 1982. The effect of microhabitat, spatial distribution, and display size on dispersal of *Lindera benzoin* by avian frugivores. – Can. J. Bot. 60: 557–560.

Murray, K. G., Winnett Murray, K., Cromie, E. A., Minor, M. and Meyers, E. 1993. The influence of seed packaging and fruit color on feeding preferences of American Robins. – Vegetatio 107/108: 217–226.

Puckey, H. L., Lill, A. and O'Dowd, D. J. 1996. Fruit color preferences of captive silvereyes (*Zosterops lateralis*). – Condor 98: 780–790.

Ridley, H. N. 1930. The dispersal of plants throughout the world. – L. Reeve & Co., Ashford, England.

Sallabanks, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. – Ecology 74: 1326–1336.

Sargent, S. 1990. Neighborhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). – Ecology 71: 1289–1298.

SAS 1989. SAS user's guide: statistics. – SAS Inst. Inc., Carey, NC.

Shaw, R. G. and Mitchell-Olds, T. 1993. ANOVA for unbalanced data: an overview. – Ecology 74: 1638–1645.

Snow, D. W. 1971. Evolutionary aspects of fruit-eating by birds. – Ibis 113: 194–202.

Stephens, D. W. and Krebs, J. R. 1986. Foraging theory. – Princeton Univ. Press, Princeton, NJ.

Tappeiner, J. C. and Zasada, J. C. 1993. Establishment of salmonberry, salal, vine maple, and bigleaf maple seedlings in the coastal forests of Oregon. – Can. J. Forest Res. 23: 1775–1780.

Tappeiner, J. C., Zasada, J. C., Ryan, P. and Newton, M. 1991. Salmonberry clonal and population structure: the basis for a persistent cover. – Ecology 72: 609–618.

Thebaud, C. and Debussche, M. 1992. A field test of the effects of infructescence size on fruit removal by birds in *Viburnum tinus*. – Oikos 65: 391–394.

Thompson, J. N. 1994. The coevolutionary process. – Univ. of Chicago Press, Chicago.

Traveset, A. and Willson, M. F. In press. Ecology of the fruit-color polymorphism in *Rubus spectabilis*. – Evol. Ecol.

Traveset, A. and Willson, M. F. 1997. Effect of birds and bears on seed germination of fleshy-fruited plants in temperate rainforests of southeast Alaska. – Oikos 80: 89–95.

Turcek, F. J. 1963. Color preference in fruit- and seed-eating birds. – Proc. XIII Int. Ornithol. Congr., pp. 285–292.

Wheelwright, N. T. 1985. Fruit size, gape width, and the diets of fruit-eating birds. – Ecology 66: 808–818.

Wheelwright, N. T. and Janson, C. H. 1985. Colors of fruit displays of bird-dispersed plants in two tropical forests. – Am. Nat. 126: 777–799.

Whelan, C. J. and Willson, M. F. 1994. Fruit choice in migrating North American birds: field and aviary experiments. – Oikos 71: 137–151.

Willson, M. F. 1983. Natural history of *Actaea rubra*: fruit dimorphism and fruit seed predation. – Bull. Torrey Bot. Club 110: 298–303.

Willson, M. F. 1986. Avian frugivory and seed dispersal in eastern North America. – In: Johnson, R. F. (ed.), Current ornithology, Vol. 3. Plenum Press, New York.

Willson, M. F. 1994. Fruit choices by captive American robins. – Condor 96: 494–502.

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

Willson, M. F. and O'Dowd, D. J. 1989. Fruit color polymorphism in a bird dispersed shrub (*Rhagodia parabolica*) in Australia. – Evol. Ecol. 3: 40–50.

Willson, M. F. and Whelan, C. J. 1990. The evolution of fruit color in fleshy fruited plants. – Am. Nat. 136: 790–809.

Willson, M. F. and Whelan, C. J. 1993. Variation of dispersal phenology in a bird-dispersed shrub, *Cornus drummondii*. – Ecol. Monogr. 63: 151–172.

Willson, M. F. and Comet, T. C. 1993. Food choices by Northwestern Crows: experiments with captive, free-ranging, and hand-raised birds. – Condor 95: 596–615.

Willson, M. F., Irvine, A. K. and Walsh, N. G. 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. – Biotropica 21: 133–147.

Willson, M. F., Graff, D. A. and Whelan, C. J. 1990. Color preferences of frugivorous birds in relation to the colors of fleshy fruits. – Condor 92: 545–555.

Zar, J. H. 1984. Biostatistical analysis, 2nd ed. – Prentice-Hall, Englewood Cliffs, NJ.

Zasada, J. C., Tappeiner, J. C., Maxwell, B. D. and Radwan, M. A. 1994. Seasonal changes in shoot and root production and in carbohydrate content of salmonberry (*Rubus spectabilis*) rhizome segments from the central Oregon Coast Ranges. – Can. J. For. Res. 24: 272–277.