

The Changing Floral Color Landscape Across an Alpine Elevation Gradient

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Abstract

Flowers at high elevation must deal with less than ideal conditions, both abiotic and biotic. A limiting biotic factor plants must cope with at high elevations is pollinator limitation. With increasing elevation, insect groups such as Hymenoptera decrease with abundance whereas the abundance of Dipteran as a group remains the same. Thus, there is a shift in the dominant pollinator guild with increasing elevation: bees are predominant at lower elevations and with increasing elevation flies predominate. With this pollinator shift there could be a corresponding shift in floral color composition of communities with increasing elevation. Using spectral analysis we found that with increasing elevation there is a significant decrease in violet and blue-flowered species and a significant increase in green, yellow, orange and red flowered species. In our initial analysis of both bee and vision space we have evidence that pollinators may be able to distinguish these changes in floral color composition in communities of different elevations.

Introduction

Understanding how biotic and abiotic factors influence species distributions and community composition has been an important ecological research topic for quite some time (Pellisier et. al 2012). Gradient studies have become a popular technique to examine how abiotic factors such as precipitation, soil conditions, altitude and latitude affect plant species distribution and communities (Dalrymple et al 2015, Gentry 1998). In these environmental gradient studies, there is generally a replacement of species by other species as environmental conditions change. This observation is known as habitat filtering a process by which environmental conditions can act as a filter for the community and dictate which species will be able to persist (Pellisier et al 2012).

In mountainous systems, elevation is an important gradient that influences plant species composition. With increasing elevation, plants are faced with harsher conditions: high wind speeds, desiccation and increased ultraviolet exposure (Arnold et al 2009). In addition to these abiotic factors, pollinator limitation may also play an important role in the composition of flowering plant species distribution across an elevational gradient. Similar to plants, pollinator composition changes with increasing altitude, as certain insect groups are better able to function at higher elevations. In a previous study (Kearns 1992), conducted in the same area as our study (Gothic, CO), it was found that overall insect abundance decreases with increasing elevation.

However, Dipteran abundance remained the same with increasing elevation. Thus, due to a lack of representation of other insect taxa, flies are the more dominant pollinator guild at higher elevations, and bees appear to be the more dominant pollinator at lower elevations (Kearns 1992). This is a common pattern in many montane systems across the world including the mountainous areas of New Zealand, the Himalayas, the Alps and the Chilean Andes (Kearns 1992).

It is well supported in the literature that flower color is under selection by pollinators (Arnold et al 2009, Shrestha et al 2014, Pellisier et al. 2012). Thus, a shift in pollinator composition may lead us to expect a shift in the dominant flower color of communities with increasing elevation. The pollination syndrome hypothesis claims that distantly related flowering species have evolved similar suites of floral traits in response to different pollen vectors (Ollerton et. al 2009). There has been some debate over the validity of using the Pollination Syndrome Hypothesis as it can not be used successfully to describe either the diversity of floral phenotypes nor predict pollinators of most species (Ollerton et. al 2009). However, the observations of the Pollination Syndrome Hypothesis can appropriately be used to make a prediction of how flower color will change across elevational communities. According to the Pollination Syndrome Hypothesis flies are associated with flowers that appear white and yellow to humans whereas bees are associated with flowers that are blue (Arnold 2009). Thus, it is reasonable to predict that as the dominant pollinator guild shifts from bees at lower elevations to anthophilous flies at higher elevations, there will be a shift from predominantly more blue flowered species at lower elevations to more yellow and white flowered species at higher, alpine elevations.

It is important to take into account pollinator vision because insects do not perceive the world in the same way as humans. All insects (that have been extensively studied thus far) possess photoreceptors that are sensitive to UV with a maximum sensitivity between 330 and 375 nm (Arnold 2009). In addition to this UV receptor, bees have two other photoreceptors which are sensitive to blue and green but generally lack red receptors (Arnold 2009). Fly vision space is not as well studied as that of bees. For this study we will consider the model of the blowfly (*Lucilia sp.*) as a model for fly pollinators. *Lucilia sp.* has five photoreceptors, four of which contribute to color vision. These four photoreceptors are highly sensitive to either UV,

violet, blue or green (Troje 1993). Thus, when considering a change in flower color composition due to a pollinator shift it is more useful ecologically to consider the change with respect to pollinator vision.

There have been a few studies that have examined flower color along an elevational gradient but only a handful have worked under the motivation of pollinator shift. In a study by Kevan (1972) it was found that in the high Arctic of the Canadian Arctic Archipelago, that yellow and white flowers predominate communities at higher elevations. Flowers with yellow coloring were found to often times also reflect UV light, creating attractive patterns detectable by insect pollinators (Kevan 1972). Another study done by Shrestha et. al (2014) examined a transect in the Himalayas of Nepal. The transect ranged from 900 to 4100 m a.s.l. and covered both subtropical and subalpine environments. The study found that higher subalpine regions had more diversity of flower color than that of the lower subtropical regions. The most relevant study to our study was done by Arnold et. al (2009) in Norway. This study examined a transect covering a range between 700 and 1600 m a.s.l. The study found that with increasing elevation there was a slight increase in bee-blue-green flowers (white to humans) and a decrease in bee-blue flowers (blue or purple to humans), which followed the expectation. However, the patterns were not statistically significant.

The goal of our study was to determine if plant communities at higher elevations have a different floral color composition of those at lower elevation and if that difference is pollinator relevant. We conducted vegetation surveys along six elevational transects in order to determine community composition of areas at different elevations. This census data was then combined with a floral spectral database. In addition to examining trends in the raw spectral data, we also translated the raw spectral data to fly vision space and bee vision space to determine if changes in floral color was pollinator relevant.

Methods

Study Sites and Data Collection

Our study sites were located in the West Elk Mountains surrounding the Rocky Mountain Biological Laboratory in Gothic, CO (38.95807, -106.98853 elev. 2889 m). In order to determine the floral color composition of different communities along elevation gradients, an existing

vegetation community composition data set was combined with a floral spectral reflectance database.

Vegetation Community Composition Data

The vegetation community composition data set was compiled in the late summer (July and August) of 2014. The data set represents communities along six elevational transects. The peaks surveyed include Avery, Cinnamon, Hunter's Hill, Ruby, Teocalli and Treasury (*Fig. 1 and Table 1*). These transects represent communities between 2,700 and 4,000 m a.s.l. From the lowest point of the transect, communities were surveyed at 100 m increments of elevation. At each site a 20m vertical transect was laid down with three 20m transects laid perpendicularly across the original transect at 0, 10, and 20m along said transect. Every 2.5m (starting at 0m) of the horizontal and vertical transects were analyzed for cover using a 20x20cm quadrat. The intersections of the vertical and horizontal transects were analyzed for cover only once (e.g. the top horizontal and vertical transects met at 10 and 0m, respectively, so the cover was only recorded at that point once). This resulted in 33 20x20cm plots in total.

Floral Spectral Database

A floral spectral database consisting of 201 of the animal pollinated-species (*table 2*) found in the vegetation community composition database was compiled. The majority of these species were collected from the area surrounding the Gothic town site as well as the original Lynn plots. About 24 of the species could not be collected due to early or late flowering times that were outside the range of the study. For each species three individual flowers were collected as well as a voucher specimen deposited in the RMBL herbarium. Within 12 hours of collection spectrometer readings were taken using an Avantes spectrometer (model 2048). Three spectral readings were taken per flower at different 'zones': zone one at the center, zone two at the middle of the petal and zone three at the tip of the petal. Only the dominant color (identified as the zone with the greatest surface area) was used for analysis. Floral measurements were also taken for each collected specimen. These measurements included display height (the height from the base of the plant to the tallest flower), flower volume and if possible inflorescence volume.

Analysis

Raw Spectral Data

We calculated community weighted mean (CWM) reflectance for raw spectra binned arbitrarily into red (625-700 nm), orange (590-625 nm), yellow (565-590 nm), green (500-565 nm), blue (440-500 nm), violet (400-440 nm), UVA (315- 400 nm), and UVB (300-315 nm). First, we calculated the absolute percent cover for each species at each site (averaged across the 33 quadrats). We then removed wind-pollinated species, non-angiosperm species (e.g. mosses) and bare ground to calculate absolute percent cover of animal-pollinated species at each site. This allowed the calculation of the relative percent cover of each species (relative to total animal-pollinated cover). Relative percent cover was then used to weight the average reflectance percentage for each color for each species, resulting in a CWM reflectance for each color at each site.

Across all sites, average cover of identified animal-pollinated species was 29%. We obtained floral reflectance spectra for species representing 96% of that identified animal-pollinated cover (corresponding to 107 of 132 species). The remaining cover consisted of wind-pollinated species and non-angiosperms, 26%; bare ground, 39%; unidentified species, 6%.

Pollinator Vision

In order to convert raw spectra into pollinator-relevant variables, we utilized *pavo*, an R package. Using the *vismodel* function in *pavo*, visual systems can be incorporated in the modeling of the raw spectral data (Maia et. al 2013). In our analysis we considered the visual systems of *Bombus sp.* and *Musca sp.* For the *Bombus* data set, we used *pavo* to determine the CWM average reflectance within the UV range, blue range and green range that bee photoreceptors are sensitive to. In order to model *Musca* vision space we followed the model of blowflies, *Lucilia sp.* as used by Troje (1993), replacing the photoreceptor sensitivity zones of *Lucilia sp.* Photoreceptors with that of *Musca*. According to this model, flies have 4 photoreceptors that contribute to color vision: R7p, R7y, R8p and R8y. These photoreceptors interact such that flies can discriminate four colors with relatively broad ranges of wavelength (Troje 1993). These four discriminatory color ranges can then be plotted on a four quadrant plot in which the x-axis is a measure of R7p –R8p and the y-axis is a measure of R7y- R8y (Troje 1993). Each quadrant represent the four color ranges that flies can distinguish: fly- UV (P+y+), fly-blue (p-y+), fly-yellow (p-y-) and fly- purple (p+y-) (*Figure 2*). For the purposes of this paper only the changes of the X and Y axes were determined with respect to elevational change.

Statistical analysis

All statistical analyses were performed in R (citation). We used the nlme package to perform linear regressions with color as the response variable. Two models were used to fit the regression for each color. In model one each peak was allowed to have a different intercept for the slope of the trend line representing the relationship between color reflectance and elevation, however the slope of the line was constrained so that each peak had the same slope. In model two each peak was to have its own unique slope and intercept. The two models were compared for each color and the model that best fit the data was then plotted. Results are plotted as partial regression plots, in which the relationship between elevation and CWM reflectance is plotted after accounting for the random effect of transect (i.e., peak).

Results

Change in Color with Elevation: Raw Spectra

We first compared the degree to which elevation affected the CWM reflectance for red, orange, yellow, green, blue, violet, UVA, and UVB. With increasing elevation the presence of red (p 0.034), orange (p 0.007), yellow (p 0.004) and green (p 0.008) flowers increased significantly (Fig 3 a-d). The presence of violet and blue colored flowering species decreased significantly with increasing elevation (Fig 3 e,f; violet (p < 0.001) and blue p < 0.001). Species with UVA coloring also decreased with increasing elevation, but this trend was not statistically significant (p 0.153) (Fig 3 g). UVB colored species showed no statistical difference in presence with change in elevation (p 0.392 (Fig 3 h). We also looked at how brightness was affected with elevation. In this analysis we considered the average reflectance across all spectra, disregarding color. There was no statistical difference across elevations in this analysis (p 0.156).

We also considered the CWM average reflectance of each color across all plots, disregarding elevation. The color with the highest average reflectance was red, followed by orange, yellow, green, blue, violet, UVA and UVB had the lowest (Fig 4). However, these differences do not appear to be statistically significant.

Change in Color with Elevation: Bombus Vision Space

With increasing elevation there is a significant decrease in the CWM average reflectance within the *Bombus* UV range (p value 0.000) as well as in the *Bombus* blue range (p value 0.000). There was no significant difference in the CWM average reflectance of the *Bombus* green range.

Change in Color with Elevation: Musca Vision Space

In this preliminary study we analyzed the X and Y axis of the *Musca* vision space using. There was a statistically significant increase in the CWM reflectance of colors that fall within the X-axis of the *Musca* vision model (p value 0.000). There was a statistically significant decrease in the Y axis (p value 0.002).

Discussion

In this preliminary study, the data set supports our prediction that there is a change in the floral color composition within communities with increasing elevation. Considering, the human vision analysis, there were several significant changes in color with varying elevation. As predicted, with increasing elevation there was a decrease in violet flowers and an increase in yellow flowers. When considering pollinator vision, there does seem to be a perceivable change in the composition of floral color with increasing elevation. There was a significant change in the excitation of both the UV and blue- sensitive photoreceptors in flowers with increasing elevation. This is indication that bees are most likely seeing a difference in the floral community with increasing elevation. Our analysis of *Musca* vision space is not as informative. We found a change in the excitation on the X and Y axis of the fly vision space model. This could mean that something is changing in the floral community of different elevations with increasing elevations for flies. However, these changes in the X and Y axes may not be significant as flies are unable to differentiate intensity (Troje 1993).

These results do not conclusively support that the change in floral color composition of communities of different elevations are relevant to pollinators, more specifically flies. In order to be able to confidently conclude that these changes are distinguishable by pollinators, future work will include plotting the spectral database on the bee color hexagon (Chittka 1992) as well as the fly vision space model (Troje 1993). This analysis will determine if there is a change in the colors distinguishable to bees and flies.

The change in composition of floral color with changing elevation could also be influenced by environmental conditions. Different pigments can provide protection from UV damage, herbivory and desiccation (Arnold et. al 2009). For example, anthocyanins are often times responsible for red, blue and purple coloration in plant parts (Chalker-Scott 1999). Anthocyanins absorb large amounts of light in the UV range which has lead to a hypothesis that the presence of anthocyanins may protect plants against damage caused by UV radiation such as DNA degradation (Woodall and Stewart 1998). Thus, it may be advantageous for plants of higher elevation to have to have anthocyanins as they are exposed to more UV. This could explain the significant increase in red coloration with increasing elevation.

Our study has revealed that there is a change in the floral color composition of communities of differing elevational communities. It has been determined that bees and flies may be able to perceive these changes. In order to confidently make a conclusion as to whether the change in floral color composition is relevant to pollinators further analysis of bee and fly vision space is necessary.

Literature Cited

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Appendix

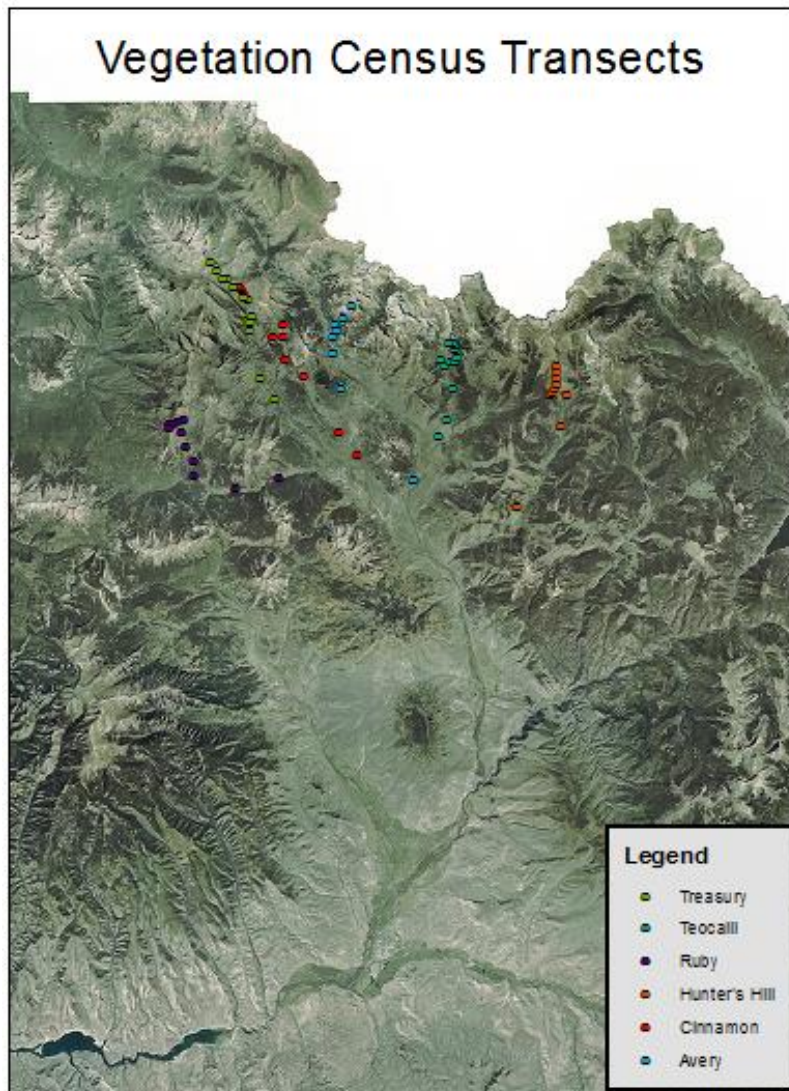


Figure 1. The figure above represents the six elevational transects surveyed in the vegetation census dataset.

Table 1. GPS location and elevations of each community surveyed in the vegetation census data set.

Peak	Site	Latitude	Longitude	Elevation (m)
Avery	27	38.8654827	-106.9123563	2710.5025
Avery	28	38.86523	-106.91238	2812
Avery	29	38.9513624	-106.9863592	2896.4175
Avery	30	38.9622425	-106.985455	2982.13
Avery	31	38.9659359	-106.982807	3134.7625
Avery	32	38.9714197	-106.9842817	3191.8475
Avery	33	38.9752925	-106.978265	3347.4425
Avery	34	38.927405	-106.97823	3454.7875

Avery	36	38.984065	-106.9702125	3655.3075
Cinnamon	27	38.88163	-106.96172	2749
Cinnamon	28	38.8972697	-106.9789927	2798.6775
Cinnamon	29	38.9345981	-107.0107845	2932.0275
Cinnamon	30	38.9453986	-107.0282175	3024.93
Cinnamon	31	38.9616842	-107.0309109	3180.5775
Cinnamon	32	38.9618937	-107.0387891	3223.2675
Cinnamon	33	38.970175	-107.029545	3366
Cinnamon	34	38.9911075	-107.0649675	3415.5
Cinnamon	35	38.99356	-107.06754	3578.5
Cinnamon	36	38.9946325	-107.06913	3664.75
Cinnamon	37	38.99495	-107.0704268	3726
Hunter's Hill	28	38.8475871	-106.819641	2824.2
Hunter's Hill	30	38.9036597	-106.7838279	3059.585
Hunter's Hill	31	38.9253823	-106.7777649	3171.2075
Hunter's Hill	32	38.9259574	-106.792322	3248.9225
Hunter's Hill	33	38.926825	-106.7910531	3321.66
Hunter's Hill	34	38.9296308	-106.7889559	3429.686667
Hunter's Hill	35	38.9329698	-106.7869929	3531.3625
Hunter's Hill	36	38.9376218	-106.7874201	3629.46
Hunter's Hill	37	38.9408429	-106.7877554	3723.5075
Hunter's Hill	38	38.9459484	-106.7877274	3827.1125
Ruby	28	38.8643025	-107.031725	2822
Ruby	29	38.856165	-107.0695375	2945
Ruby	30	38.864465	-107.10579	3054.5
Ruby	31	38.874205	-107.1059775	3128.25
Ruby	32	38.8838225	-107.11328	3199.25
Ruby	33	38.8945358	-107.117217	3332.75
Ruby	34	38.9022645	-107.1162982	3447.25
Ruby	35	38.901041	-107.1219444	3539
Ruby	36	38.8999706	-107.1257951	3633.25
Ruby	37	38.8991597	-107.1283646	3723
Ruby	38	38.8973165	-107.1280478	3833
Teocalli	27	38.8957149	-106.8912166	2775.5225
Teocalli	28	38.906143	-106.8838351	2867.8875
Teocalli	29	38.9287655	-106.8784469	2947.5225
Teocalli	30	38.9440396	-106.8871652	3046.6125
Teocalli	31	38.9481471	-106.8901588	3157.2825
Teocalli	32	38.9475785	-106.880713	3274.9425
Teocalli	33	38.9472023	-106.8775578	3351.3175
Teocalli	34	38.9503445	-106.8761911	3443.385
Teocalli	35	38.9534378	-106.8762902	3553.005
Teocalli	36	38.9559274	-106.8779412	3667.31
Teocalli	37	38.9581807	-106.8779317	3771.4975
Teocalli	38	38.9591946	-106.8800653	3878.885
Teocalli	39	38.9599953	-106.8827217	3954.33
Treasury	27	38.9186175	-107.0362825	2747.435
Treasury	28	38.93282	-107.0497925	2794.935
Treasury	29	38.9725825	-107.0618628	2971.83
Treasury	30	38.96515	-107.0594325	3038.2575
Treasury	32	38.9707325	-107.0587125	3197.25
Treasury	32.5	38.97579	-107.0585325	3256.5
Treasury	33.5	38.9861725	-107.06182	3371
Treasury	34	38.98793	-107.0649775	3418.25
Treasury	35	38.9957425	-107.07463	3521

Treasury	36	39.0000025	-107.08065	3598
Treasury	37	38.9999325	-107.0842975	3697.75
Treasury	38	39.005835	-107.0908275	3814.5
Treasury	40	39.0113075	-107.095645	4023.25

Table 2. The following table lists the species present in the floral spectral database used for analysis. The FSD # is a unique number we assigned to each species.

Family	Species Name	FSD #
Apiaceae	Cymopterus lemonii	42
Apiaceae	Heracleum sphondylium	87
Apiaceae	Ligusticum porteri	61
Apiaceae	Osmorhiza occidentalis	26
Asteraceae	Achillea millefolium	95
Asteraceae	Agoseris aurantiaca	68
Asteraceae	Agoseris glauca	3
Asteraceae	Anaphalis margaritacea	312
Asteraceae	Antennaria parvifolia	8
Asteraceae	Antennaria rosea	207
Asteraceae	Arnica cordifolia	72
Asteraceae	Arnica longifolia	295
Asteraceae	Arnica mollis	104
Asteraceae	Arnica parryi	110
Asteraceae	Artemisia cana	125
Asteraceae	Artemisia dracunculus	116
Asteraceae	Artemisia scopulorum	290
Asteraceae	Artemisia tridentata	297
Asteraceae	Aster ascendens	124
Asteraceae	Aster engelmannii	112
Asteraceae	Aster lanceolatus	120
Asteraceae	Balsamorhiza sagittata	1
Asteraceae	Chaenactis alpina	279
Asteraceae	Chaenactis douglasii	250
Asteraceae	Chrysothamnus depressus	106
Asteraceae	Chrysothamnus viscidiflorus	107
Asteraceae	Cirsium eatonii	115
Asteraceae	Crepis acuminata	82
Asteraceae	Crepis intermedia	81
Asteraceae	Ericameria parryi	122
Asteraceae	Erigeron coulteri	101
Asteraceae	Erigeron elatior	75

Asteraceae	<i>Erigeron flagellaris</i>	9
Asteraceae	<i>Erigeron glacialis</i>	263
Asteraceae	<i>Erigeron melanocephalus</i>	291
Asteraceae	<i>Erigeron pinnatisectus</i>	229
Asteraceae	<i>Erigeron speciosus</i>	93
Asteraceae	<i>Erigeron vagus</i>	239
Asteraceae	<i>Helianthella quinquenervis</i>	59
Asteraceae	<i>Heliomeris multiflora</i>	309
Asteraceae	<i>Heterotheca villosa</i>	98
Asteraceae	<i>Hymenoxys grandiflora</i>	240
Asteraceae	<i>Hymenoxys hoopesii</i>	90
Asteraceae	<i>Ligularia amplexans</i>	268
Asteraceae	<i>Ligularia holmii</i>	287
Asteraceae	<i>Machaeranthera canescens</i>	109
Asteraceae	<i>Packera streptanthifolia</i>	36
Asteraceae	<i>Packera wernerifolia</i>	233
Asteraceae	<i>Psilochenia occidentalis</i>	51
Asteraceae	<i>Pyrrocoma crocea</i>	97
Asteraceae	<i>Rudbeckia hirta</i>	305
Asteraceae	<i>Senecio atratus</i>	247
Asteraceae	<i>Senecio bigelovii</i>	261
Asteraceae	<i>Senecio crassulus</i>	70
Asteraceae	<i>Senecio fremontii</i>	278
Asteraceae	<i>Senecio integerrimus</i>	4
Asteraceae	<i>Senecio serra</i>	123
Asteraceae	<i>Senecio soldanella</i>	281
Asteraceae	<i>Solidago multiradiata</i>	308
Asteraceae	<i>Solidago parryi</i>	117
Asteraceae	<i>Solidago simplex</i>	244
Asteraceae	<i>Taraxacum eriophorum</i>	294
Asteraceae	<i>Taraxacum officinale</i>	296
Asteraceae	<i>Tetradymia canescens</i>	108
Asteraceae	<i>Tragopogon dubius</i>	204
Asteraceae	<i>Viguiera multiflora</i>	92
Asteraceae	<i>Wyethia x magna</i>	260
Berberidaceae	<i>Mahonia repens</i>	16
Boraginaceae	<i>Hackelia floribunda</i>	153
Boraginaceae	<i>Mertensia ciliata</i>	30
Boraginaceae	<i>Mertensia lanceolata</i>	24
Brassicaceae	<i>Arabis drummondii</i>	35
Brassicaceae	<i>Barbarea orthoceras</i>	54

Brassicaceae	<i>Cardamine cordifolia</i>	212
Brassicaceae	<i>Descurainia pinnata</i>	56
Brassicaceae	<i>Draba albertina</i>	22
Brassicaceae	<i>Draba crassa</i>	316
Brassicaceae	<i>Draba reptans</i>	285
Brassicaceae	<i>Draba spectabilis</i>	41
Brassicaceae	<i>Erysimum capitatum</i>	33
Brassicaceae	<i>Noccaea fendleri</i>	286
Brassicaceae	<i>Noccaea montana</i>	19
Brassicaceae	<i>Thlaspi arvense</i>	63
Campanulaceae	<i>Campanula parryi</i>	213
Campanulaceae	<i>Campanula rotundifolia</i>	99
Campanulaceae	<i>Campanula uniflora</i>	292
Caprifoliaceae	<i>Lonicera involucrata</i>	55
Caprifoliaceae	<i>Sambucus racemosa</i>	158
Caprifoliaceae	<i>Symphoricarpos oreophilus</i>	50
Caryophyllaceae	<i>Arenaria congesta</i>	46
Caryophyllaceae	<i>Cerastium beeringianum</i>	293
Caryophyllaceae	<i>Silene acaulis</i>	280
Caryophyllaceae	<i>Stellaria longipes</i>	76
Celastraceae	<i>Paxistima myrsinites</i>	218
Chenopodiaceae	<i>Chenopodium atrovirens</i>	121
Crassulaceae	<i>Sedum integrifolium</i>	58
Crassulaceae	<i>Sedum lanceolatum</i>	77
Ericaceae	<i>Vaccinium cespitosum</i>	73
Ericaceae	<i>Vaccinium myrtillus</i>	159
Fabaceae	<i>Astragalus alpinus</i>	307
Fabaceae	<i>Astragalus robbinsii</i>	217
Fabaceae	<i>Hedysarum boreale</i>	216
Fabaceae	<i>Lathyrus lanszwertii</i>	14
Fabaceae	<i>Lupinus argenteus</i>	269
Fabaceae	<i>Lupinus bakeri</i>	27
Fabaceae	<i>Oxytropis borealis</i>	231
Fabaceae	<i>Oxytropis deflexa</i>	236
Fabaceae	<i>Oxytropis lambertii</i>	80
Fabaceae	<i>Trifolium repens</i>	111
Fabaceae	<i>Vicia americana</i>	49
Fumariaceae	<i>Corydalis caseana</i>	57
Gentianaceae	<i>Gentiana parryi</i>	119
Gentianaceae	<i>Gentianella acuta</i>	113
Gentianaceae	<i>Gentianella heterosepala</i>	311

Gentianaceae	Gentianopsis thermalis	152
Gentianaceae	Frasera speciosa	201
Geraniaceae	Geranium richardsonii	66
Geraniaceae	Geranium viscosissimum	303
Grossulariaceae	Ribes cereum	156
Grossulariaceae	Ribes montigenum	44
Grossulariaceae	Ribes wolfii	157
Hydrophyllaceae	Hydrophyllum capitatum	21
Hydrophyllaceae	Hydrophyllum fendleri	28
Hydrophyllaceae	Phacelia hastata	215
Hydrophyllaceae	Phacelia sericea	232
Iridaceae	Sisyrinchium strictum	306
Lamiaceae	Agastache urticifolia	94
Lamiaceae	Prunella vulgaris	277
Liliaceae	Allium geeyeri	12
Liliaceae	Calochortus gunnisonii	78
Liliaceae	Erythronium grandiflorum	17
Liliaceae	Lloydia serotina	238
Liliaceae	Maianthemum stellatum	210
Liliaceae	Streptopus amplexifolius	249
Liliaceae	Veratrum californicum	276
Liliaceae	Zigadenus elegans	155
Linaceae	Linum lewisii	60
Onagraceae	Epilobium saximontanum	53
Onagraceae	Gayophytum diffusum	86
Onagraceae	Chamerion angustifolium	151
Polemoniaceae	Collomia linearis	64
Polemoniaceae	Ipomopsis aggregata	65
Polemoniaceae	Ipomopsis tenuituba	254
Polemoniaceae	Phlox multiflora	10
Polemoniaceae	Polemonium foliosissimum	88
Polemoniaceae	Polemonium pulcherrimum	43
Polemoniaceae	Polemonium viscosum	314
Polygonaceae	Eriogonum coloradense	230
Polygonaceae	Eriogonum racemosum	79
Polygonaceae	Eriogonum umbellatum	39
Polygonaceae	Eriogonum umbellatum	52
Polygonaceae	Polygonum bistortoides	253
Polygonaceae	Polygonum douglasii	48
Polygonaceae	Polygonum polygaloides	114
Portulacaceae	Claytonia lanceolata	25

Portulacaceae	Oreobroma pygmaea	252
Primulaceae	Androsace septentrionalis	11
Primulaceae	Dodecatheon pulchellum	202
Pyrolaceae	Pyrola rotundifolia	264
Ranunculaceae	Aconitum columbianum	206
Ranunculaceae	Anemone multifida	71
Ranunculaceae	Anemone narcissiflora	289
Ranunculaceae	Anemone patens	227
Ranunculaceae	Aquilegia coerulea	85
Ranunculaceae	Aquilegia elegantula	208
Ranunculaceae	Caltha leptosepala	275
Ranunculaceae	Delphinium barbeyi	62
Ranunculaceae	Delphinium nuttallianum	2
Ranunculaceae	Ranunculus alismifolius	6
Ranunculaceae	Ranunculus inamoenus	18
Ranunculaceae	Thalictrum fendleri	219
Rosaceae	Amelanchier alnifolia	38
Rosaceae	Fragaria virginiana	45
Rosaceae	Geum rossii	221
Rosaceae	Geum triflorum	222
Rosaceae	Ivesia gordonii	226
Rosaceae	Potentilla diversifolia	272
Rosaceae	Potentilla fruticosa	118
Rosaceae	Potentilla gracilis	7
Rosaceae	Potentilla hippiana	265
Rosaceae	Potentilla pulcherrima	266
Rosaceae	Rosa woodsii	100
Rosaceae	Sibbaldia procumbens	251
Rubiaceae	Galium boreale	96
Saxifragaceae	Heuchera parvifolia	32
Saxifragaceae	Lithophragma glabrum	31
Saxifragaceae	Saxifraga bronchialis	214
Saxifragaceae	Saxifraga odontoloma	154
Scrophulariaceae	Castilleja linariifolia	299
Scrophulariaceae	Castilleja miniata	15
Scrophulariaceae	Castilleja occidentalis	284
Scrophulariaceae	Castilleja rhexiifolia	288
Scrophulariaceae	Castilleja sulphurea	67
Scrophulariaceae	Collinsia parviflora	40
Scrophulariaceae	Mimulus guttatus	262
Scrophulariaceae	Orthocarpus luteus	105

Scrophulariaceae	Pedicularis bracteosa	242
Scrophulariaceae	Pedicularis groenlandica	302
Scrophulariaceae	Pedicularis procera	245
Scrophulariaceae	Pedicularis racemosa	84
Scrophulariaceae	Penstemon caespitosus	5
Scrophulariaceae	Penstemon strictus	47
Scrophulariaceae	Penstemon whippleanus	74
Scrophulariaceae	Veronica americana	301
Scrophulariaceae	Veronica nutans	315
Valerianaceae	Valeriana acutiloba	23
Valerianaceae	Valeriana edulis	69
Violaceae	Viola adunca	211
Violaceae	Viola canadensis	223
Violaceae	Viola praemorsa	20
	Unidentified	29

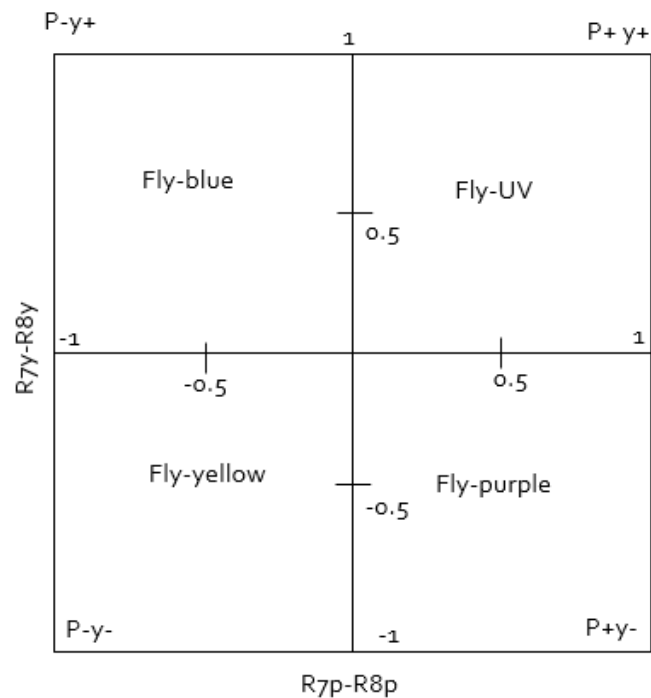


Figure 2. The plot above represents the fly vision space model (Troje 1993, Arnold et. al 2009). The model represent the inhibitory effects the four photoreceptors have on each other and how excitation of each photoreceptor results in the perception four broad color regions by flies.

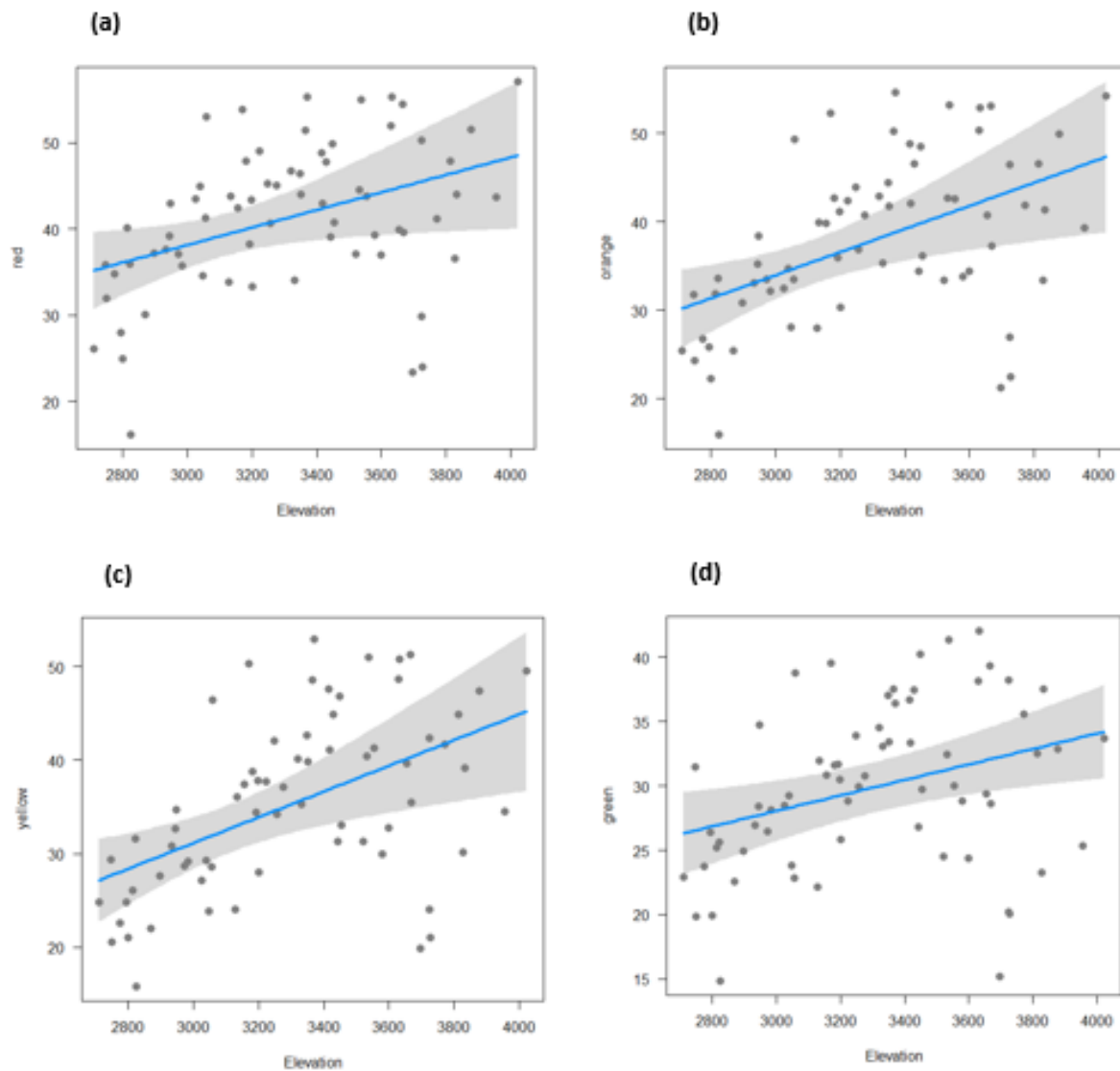


Figure 3 (a-d) The plots above are partial leverage plots for each color analyzed with elevation on the x axis.

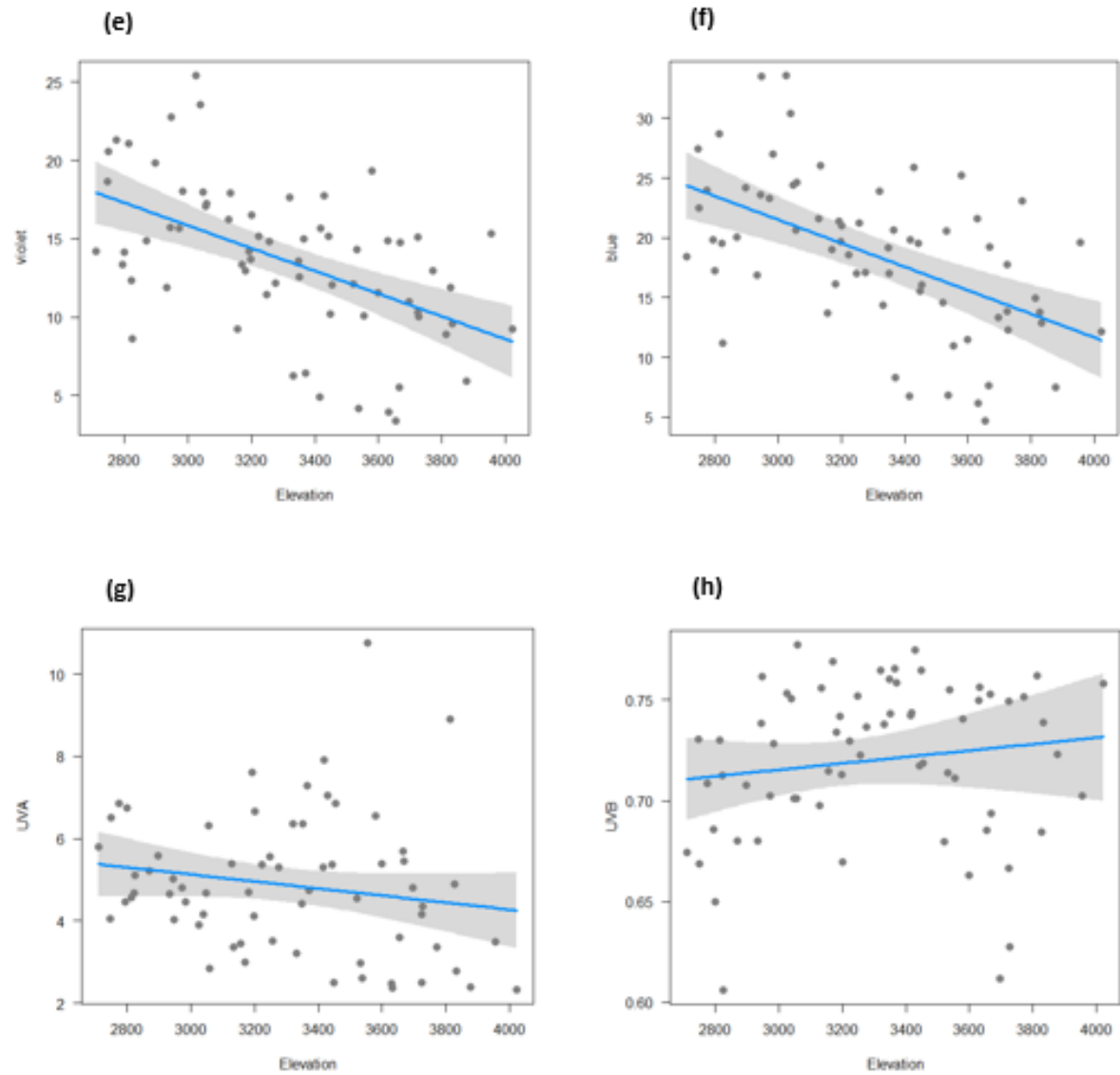


Figure 3 (e-h) The plots above are partial leverage plots for each color analyzed with elevation on the x axis.

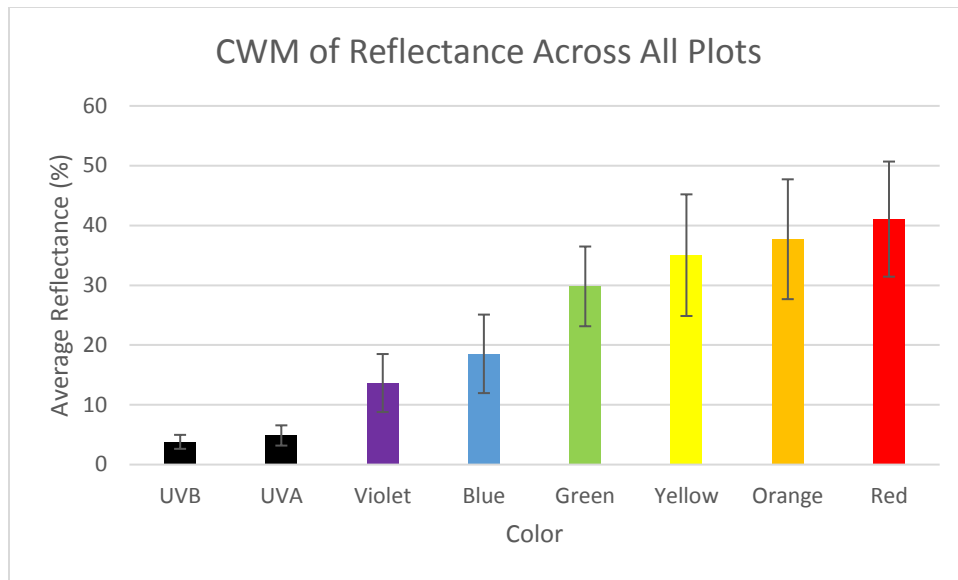


Figure 4. The bar graph represents the average reflectance of colors present across our plots, disregarding elevation.

