

The Relationships Among Butterfly Size, Visitation Rate, Handling Time, and Floral Display Size

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ABSTRACT: A complete understanding of interactions occurring at the community level in pollination networks is necessary to create better conservation policies in a rapidly changing world. Such interactions may be governed by size-based morphological characteristics of both floral displays and insect pollinators. The goal of this study was to examine the effects of butterfly size and floral display size on interactions between butterflies and floral displays. Measurements were made on both floral displays and butterflies in the lab, and individual butterflies were followed in the field to record interactions between butterflies and floral displays. Butterfly size was found to significantly influence visitation rate both within and across plant species ($p=0.0226$). Butterfly size did not significantly influence handling time though a negative relationship was apparent between butterfly size and handling time within a plant species. Floral display size did not significantly influence visitation rate ($p=0.6888$). Both nectar depth ($p=0.001$) and abundance ($p<0.001$) were found to significantly influence total number of visits. Floral display size had no definitive relationship with handling time. Exclusion of a single flowering species resulted in a significant relationship between the two variables ($p=0.034$) suggesting that more research is necessary to determine if a relationship exists. The results of this study suggest that simple size-based morphological features of both butterfly pollinators and the floral species they visit influence interactions between the two, and further research in this direction should be pursued to develop more comprehensive models.

INTRODUCTION:

Understanding relationships between plant-pollinator morphology and behavior can lead to a better comprehension of the complex interactions occurring within a community. These relationships may then be used to make predictions of the frequency and types of interactions that do occur, ultimately providing better conservation techniques. Stang et al. (2006, 2007,

2009) showed that visitor proboscis length, nectar tube depth, and relative abundance of species can be used to predict the frequency of interactions between pollinators and flowers. However, there is still some disagreement between expected and observed interactions which, as Stang (2008) suggests, could be due to a failure to capture all of the important aspects that determine plant-pollinator interactions from the pollinator's perspective. Such aspects might include the energetic cost of foraging versus the net energetic gain (Boggs 1988 and references therein), which is related to plant and/or pollinator morphology (Woodward et al. 2005). Thus, to better predict interactions at a community level, other size-based relationships should be examined, and where applicable, included in existing models.

Butterflies are frequent visitors to flowers, in search of energy and nutrient rich nectar (Corbet 2000, Bertin 1989). During foraging bouts for nectar, butterflies also transfer pollen from plant to plant, making them pollinators in mutualistic plant-pollinator networks (Waser 2007, Herrera 1987, Bertin 1989). Though frequently not as efficient as bees, butterflies are still considered important in their role as plant pollinators (Herrera 1987, Bertin 1989). Butterflies tend to visit inflorescences or flower clusters more frequently than they do solitary flowers (Corbet 2000). There is also evidence that butterflies visit large inflorescences more frequently than they do small ones (Gomez et al. 2008, Arroyo et al. 2007, Vaughton & Ramsey 1998, Schemske 1976). This may be due to the greater net energetic gains provided by large inflorescences as walking between flowers is less energetically expensive than flight (Corbet 2000) and may suggest that there is a relationship between inflorescence size and butterfly visitation rate. This is further supported by Buide (2005) who showed that plants with larger floral displays received pollinator visits more frequently than plants with smaller floral displays. As visitation rate is closely related to handling time (Corbet 2000, Herrera 1989), a relationship

may also exist between the size of the floral display and handling time. Furthermore, Herrera (1989) showed that as butterfly proboscis length increased, flower handling time in *Lavandula latifolia* decreased. This pattern has also been observed in bumblebees (Inouye 1980), though the relationship has not been extensively studied. In butterflies, proboscis length is positively correlated with body size, indicating that a negative relationship between handling time and butterfly size may exist (Knute 2007, Corbet 2000, Boggs 1988). This also suggests that there may be a relationship between butterfly size and visitation rate as visitation rate is related to handling time (Corbet 2000, Herrera 1989). Also, larger animals have higher energetic requirements than smaller animals (Peters 1983). Therefore, larger butterflies would have higher nectar requirements met by visiting more flowers and would have higher visitation rates than smaller butterflies. In this study I examine the relationships existing among butterfly size, proboscis length, handling time, visitation rate, and floral display size.

To examine these potential size-based relationships, the following hypotheses were tested in this study:

- Butterfly proboscis length, body length, and body mass are positively correlated
- As butterfly size increases, visitation rate (number of visits to floral displays per minute) will increase
- As floral display size increases, visitation rate and total number of butterfly visits to the plant species will increase
- As butterfly size increases, handling time per display (the total residence time on a display) will decrease
- As floral display size increases, handling time per display will decrease

The hypotheses in relation to visitation rate, total number of visits and handling time were first tested across all plant and butterfly species interacting in the community and second within the four most visited plant species separately. In addition, experimental size manipulations on two plant species were performed and the following hypotheses tested:

- As the size of a floral display within a plant species decreases handling time will increase
- As the size of a floral display within a plant species decreases visitation rate will decrease

MATERIALS AND METHODS:

Study site and observation period:

This study took place at the Rocky Mountain Biological Laboratory in Gothic, Gunnison County, Colorado, USA from July 6, 2009 to August 5, 2009. The study site was located in a dry rocky meadow. Pollinating insects of four orders were observed to be present in the meadow. Five families of butterflies were seen and at least seventeen species were present. There are 22 plant species flowering in the meadow during this time, 12 of which were observed to be visited by butterflies (See Appendix).

Size parameters of butterfly and plant species:

A minimum of five butterflies of each observed species were captured for morphological measurements (with the exception of rare species in which only as many butterflies as I was able to catch were measured). They were cooled down and brought to the lab where I measured proboscis length, body length, body mass, and the length of the forewing. Each butterfly was

photographed for confirmation of species identity and to determine total wing area using ImageJ software. Butterflies were then released back to the meadow.

Ten flowers or floral heads from each of the floral species visited by butterflies were collected. Total surface area of the floral display, number of open flowers or number of nectaries (single flowers), corolla diameter, nectar tube depth and nectar tube diameter were measured with digital calipers and a dissecting microscope. These measurements were made and provided by Martina Stang.

Determination of visitation rate and handling time:

I followed individual butterflies for as long as possible, recording their behavior with a digital voice recorder. I selected butterflies to be followed by entering the meadow and following the first butterfly I saw. The butterfly was then followed for as long as possible. Upon losing the butterfly I walked in a random direction until I came across another butterfly, which I would then follow for as long as possible. This process was repeated every day for a minimum of two hours, over a two week period. For each butterfly I observed, I recorded species and which floral displays were visited. I later analyzed the voice recordings to determine total time spent at each display (which I term handling time in this paper) and the number of floral displays visited per unit time. Floral abundance was determined once during the two weeks of butterfly observation by making floral counts at 36 10m² plots along a transect previously established by Martina Stang.

Experimental manipulations of floral display size:

To further evaluate the effects of floral display size on handling time and visitation rate, experimental plots using *Eriogonum umbellatum* and *Linum lewisii* were constructed.

Eriogonum umbellatum produces a compact inflorescence while *Linum lewissii* produces single flowers with five nectaries. Both were visited by a wide array of pollinators including butterflies and could easily be manipulated.

The experiment involving *Eriogonum umbellatum* consisted of six 1m×1m plots. One third of the inflorescences were enlarged in size, one third reduced in size, and the remainder served as unaltered controls. I increased the inflorescence size by bringing three floral heads of adjacent stalks together and using a twist tie to hold them in place. I decreased inflorescence size by removing three umbels unless this would remove all flowers from the plant in which case I removed all but one umbel. Plant treatments were randomly assigned. Plots were observed for one hour each, in fifteen minute increments with rotation between plots after each increment. These observations were made from 6 July 2009 through 7 July 2009, for a total of six hours of observation.

The *Linum lewisii* experiment consisted of three 60cm×80cm experimental plots, each consisting of six rows of eight flower picks spaced 10cm apart. Half of the flowers in each array were reduced through cutting half of the petals off, while the other half of the flowers remained as unaltered controls. Plants were randomly placed in the plots. The plots were then observed for five hours making recordings of visitation and handling time for all visitors. Observations were made on the 9th, 10th, and 22nd of July totaling 15 hours of observation. Butterfly visitation was too low to provide enough data for statistical analysis.

Data analysis:

Regression analyses were performed using JMP and SPSS software to evaluate relationships between floral display size and visitation rate, floral display size and handling time,

proboscis length and handling time, body size and handling time, and body size and visitation rate. All parameters were found to be normally distributed, so no transformations were done on the data. Regressions were used to evaluate relationships between butterfly size, visitation rate, and handling time, and multiple regressions were used to evaluate the influence of floral display size on visitation rate and handling time correcting for floral abundance and nectar tube depth. Though experiments yielded very low butterfly visitation, a t-test was performed to evaluate differences in handling times for the seventeen visits made by one butterfly to a *Linum lewissii* plot (Table 1).

RESULTS:

Relationships among butterfly morphological features:

There are significant positive relationships between proboscis length, body length, and body mass (Figure 1). The relationship between body length and proboscis length ($R^2=0.84$, $p<0.0001$) shows that there is little variation from the regression line with the exception of two points lying above the line. Both of these points are based on data from butterflies of the family Hesperiidae (Figure 1). Because butterflies of this family differed so much morphologically and behaviorally from the other four butterfly families (*personal observation*), they were excluded from all other analyses. Excluding Hesperiidae, the relationship between body mass and proboscis length was significant ($R^2=0.543$, $p=0.004$) as was the relationship between body mass and body length ($R^2=0.571$, $p=0.0028$).

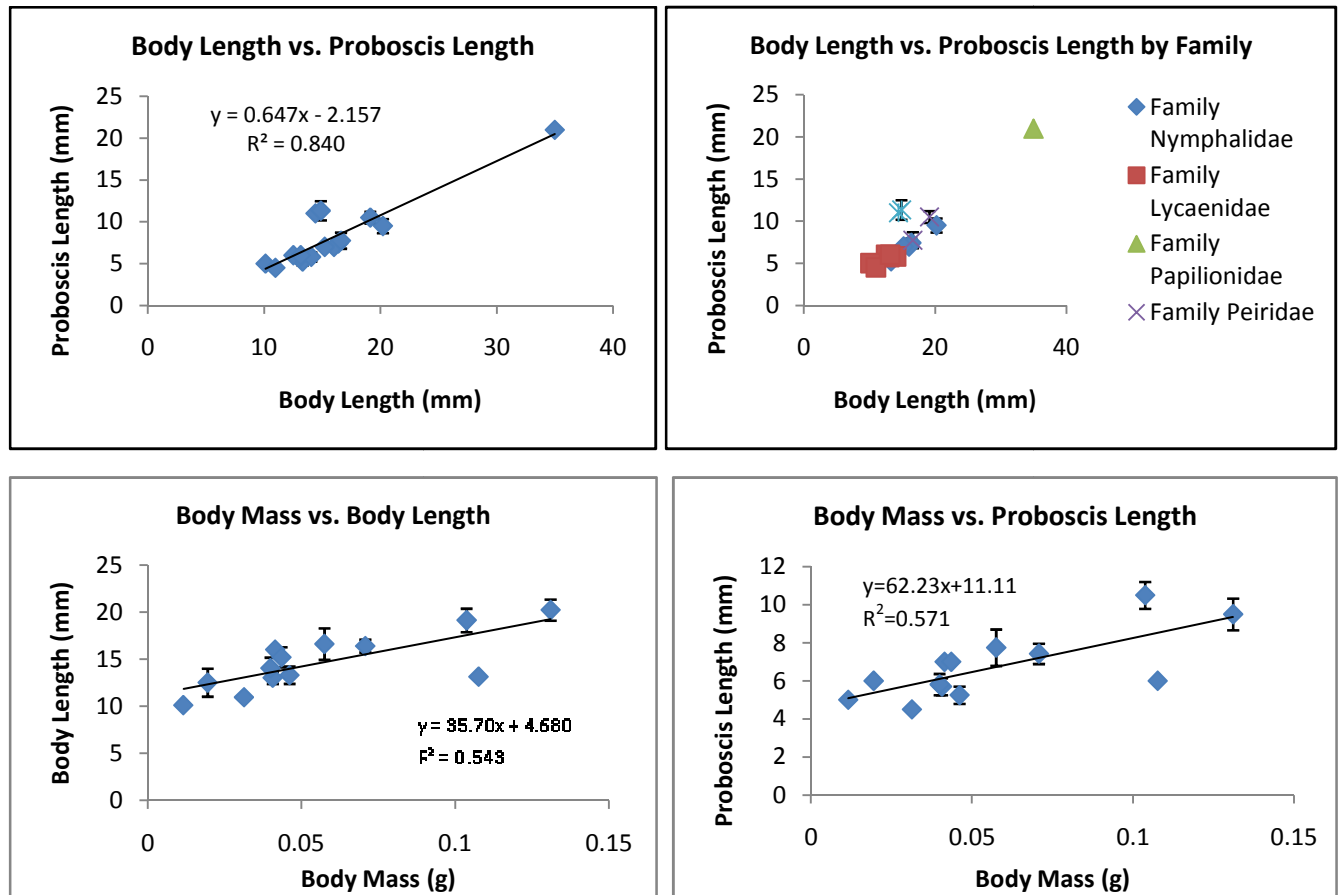


Figure 1: Relationships between butterfly body length, proboscis length, and body mass. P-values for body length vs. proboscis length, body mass vs. proboscis length, and body mass vs. body length are <0.001, 0.004, and 0.0028 respectively. The graphs for body mass vs. proboscis length and body length do not include Hesperidae data.

Size influences on visitation rate and total number of visits:

A strong positive relationship was found between butterfly body mass and visitation rate across all visited floral species (Figure 2, $R^2=0.676$, $p=0.0226$, $n=10$). Significant relationships between visitation rate and proboscis length were also found within the four most visited plant species (Figure 3). This relationship was most significant for *Arenaria congesta* ($p<0.0001$, $n=8$) and less significant for *Erigeron speciosus* ($p=0.0510$, $n=9$) and *Viguiera multiflora* ($p=0.0791$, $n=6$), while there was no significant relationship for the most visited species, *Heterotheca villosa*, though there was a positive trend ($R^2=0.252$, $n=8$).

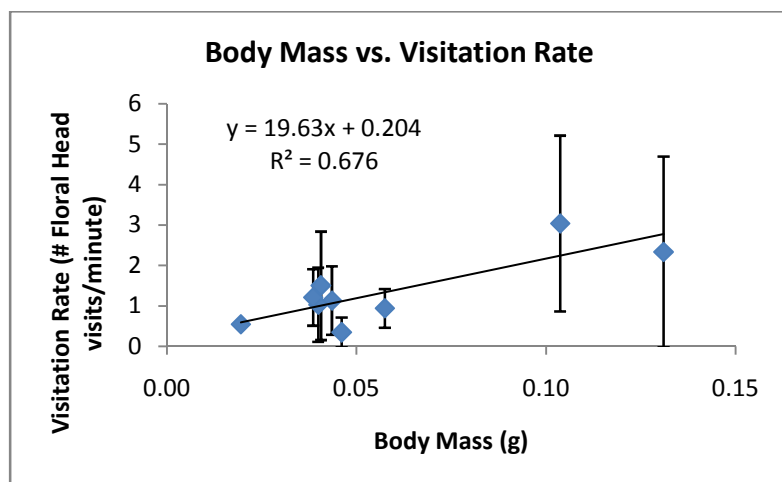


Figure 2: The relationship between butterfly body mass and visitation rate across all plant species. Each point represents average visitation rate for one species of butterfly. $P=0.0226$.

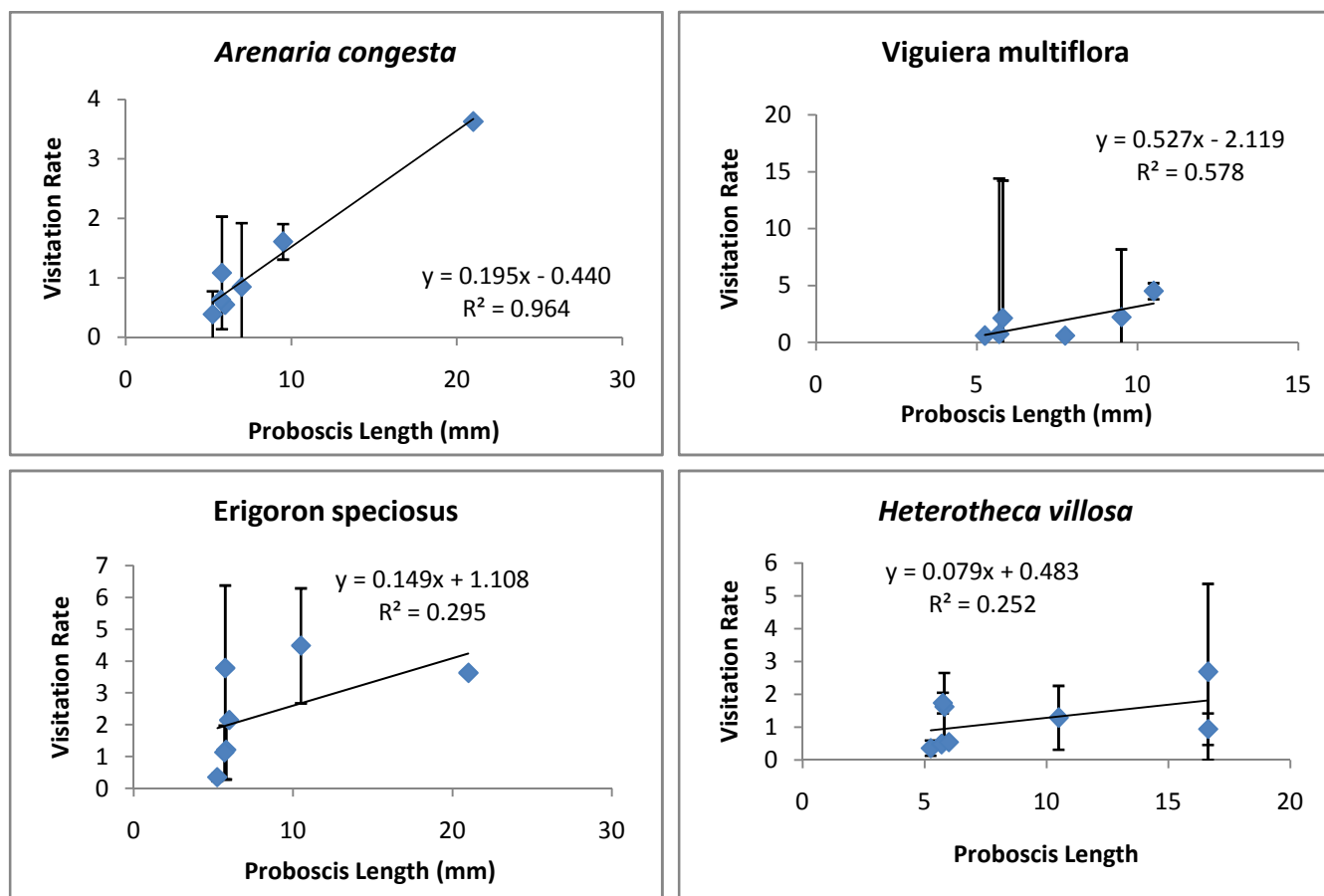


Figure 3: The relationships between butterfly proboscis length and visitation rate for the four most visited floral species (see Appendix). Each point represents the average visitation rate for a butterfly species. The relationships for *Arenaria congesta*, *Erigeron speciosus*, and *Viguiera multiflora* are significant or almost significant with p-values of <0.0001 , 0.0510, and 0.0791 respectively.

There was no relationship found between floral display size and visitation (total number of visits) across all butterfly species (Figure 4, $R^2=0.016$, $p=0.6888$, $n=12$). The only floral factors which were found to significantly impact visitation were nectar depth and floral abundance (Figure 5, Nectar Depth vs. Visitation $R^2=0.647$, $p=0.001$, $n=12$, Abundance vs. Visitation $R^2=0.700$, $p<0.001$, $n=12$). Multiple regression with these two factors explained 91.6% of the variation in visitation and was not improved with the addition of floral size. There were no relationships between floral display size and visitation within a butterfly species either (Figure 6, *Speyeria*: $R^2=0.423$, $p=0.1618$, $n=6$ *L. heteronea*: $R^2=0.155$, $p=0.3809$, $n=7$). Nectar tube depth was found to be the only significant predictor for visitation for *L. heteronea* only (Figure 7, $R^2=0.597$, $p=0.0418$, $n=7$).

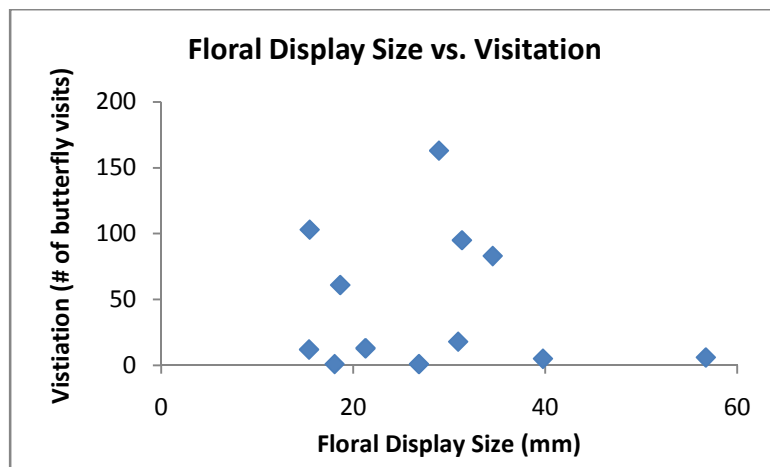


Figure 4: The relationship between floral display size and visitation across all butterfly and plant species. The relationship is non-significant, $p=0.6888$.

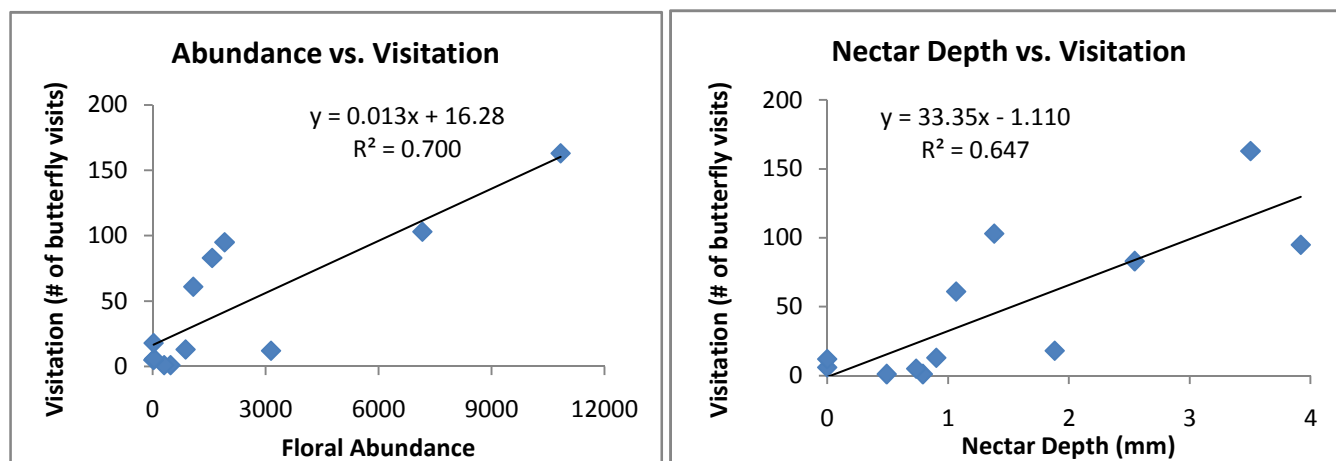


Figure 5: The relationships between nectar depth and visitation and abundance and visitation across all plant and butterfly species. Both relationships are significant with p-values of 0.001 and <0.001 respectively.

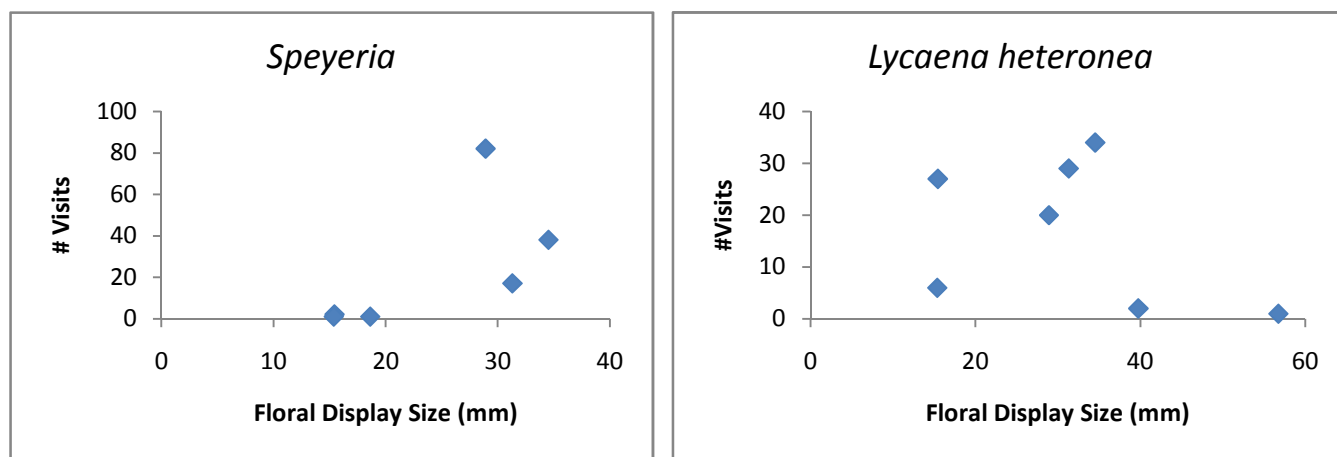


Figure 6: The relationships between floral display size and visitation for the two butterfly species/genus that visited most frequently (See Appendix). Neither relationship is significant. *Speyeria*: $R^2=0.423$, $p=0.1618$, $n=6$. *heteronea*: $R^2=0.155$, $p=0.3809$, $n=7$

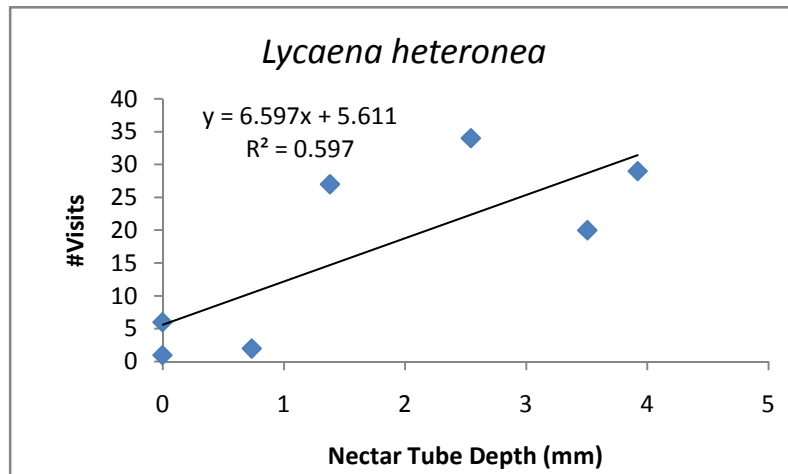


Figure 7: The relationship between visitation and nectar tube depth for the butterfly species *Lycaena heteronea*. It is the only significant factor explaining visitation, and only for this butterfly species. $R^2=0.597$, $p=0.0418$, $n=7$

Size influences on handling times:

There was no significant relationship between butterfly body mass and handling time across floral species ($R^2=0.137$, $p=0.1235$) nor between floral display size and handling time across all butterfly species ($R^2=0.068$, $p=0.4101$). There was no relationship between floral display size and handling time across butterfly species after correcting for number of open flowers (or accessible nectaries) and nectar tube depth. However, exclusion of just one floral species, *Eriogonum subalpinum*, showed a significant negative relationship between the two variables (Figure 8, $R^2=0.407$, $p=0.034$, $n=11$). There were also no relationships between floral display size and handling time within butterfly species after correcting for these factors through multiple regression (*Speyeria*: $R^2=0.370$, $p=0.2002$, $n=6$; *L. heteronea*: $R^2=0.049$, $p=0.6342$, $n=7$).

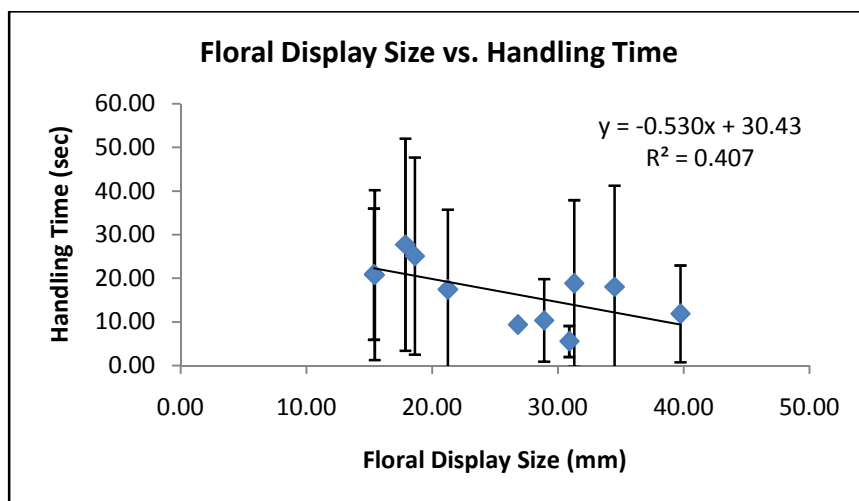


Figure 8: The relationship between floral display size and handling time after excluding *Eriogonum subalpinum*. Each point represents the average handling time for a butterfly species. $P=0.034$

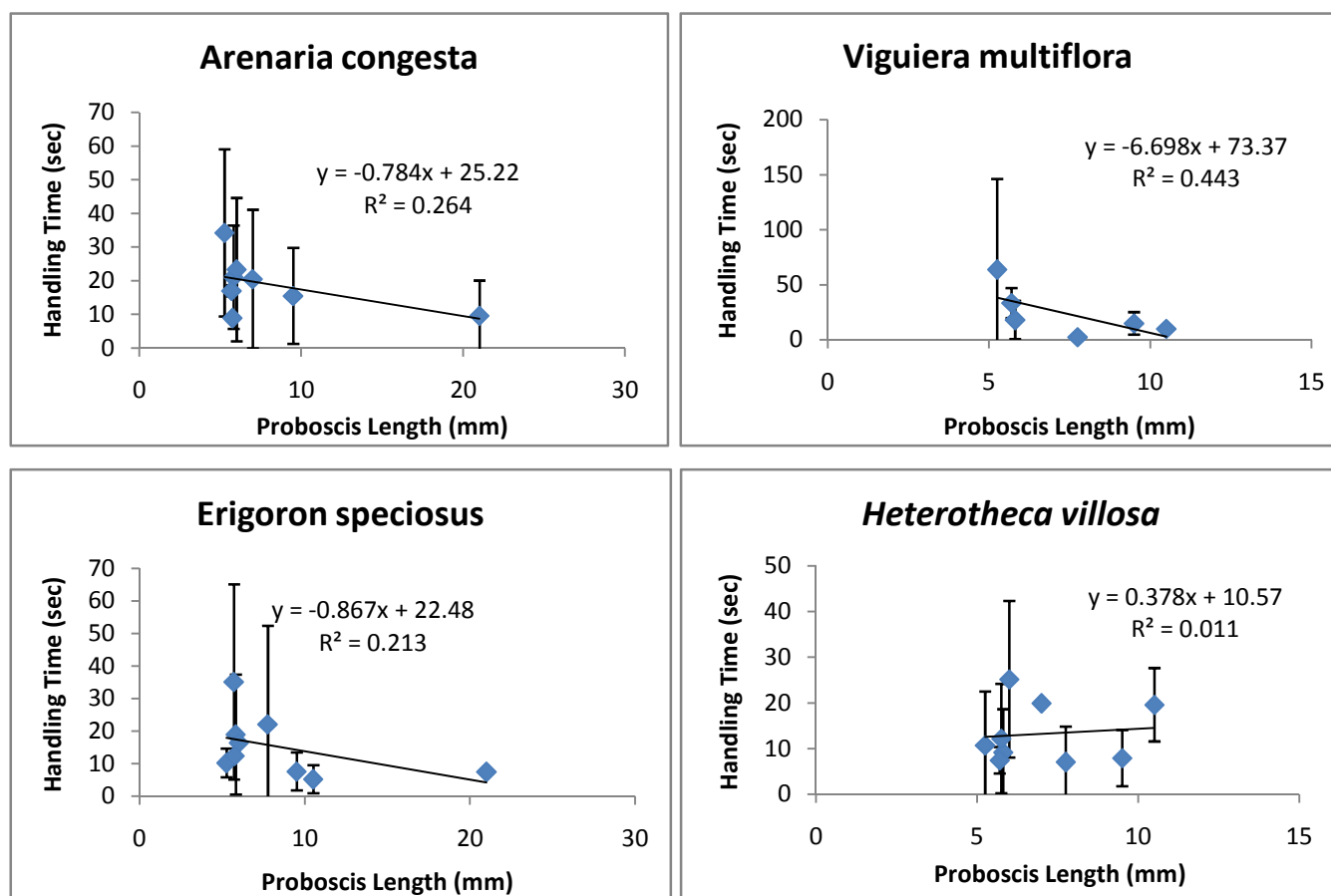


Figure 9: The relationships between butterfly proboscis length and handling time for the four most visited floral species (see Appendix). Each point represents the average handling time for a butterfly species. All relationships are non-significant.

When handling time was considered individually for the four most visited plant species, there were still no significant relationships between butterfly proboscis length and handling time, though negative relationships between the two variables were evident (Figure 9).

Experimental size manipulations on handling time and visitation rate:

Neither experiment yielded many butterfly visitations. Of the insect visitations to *Linum lewissii*, 63.9% were made to unaltered flowers while 36.1% were made to the reduced flowers (See Table 1). Solitary bees made up 57.3% of all visits, with all other insect species making up the remaining 42.7% of visits. Butterflies (including Hesperiiidae) made up only 4.8% of all visits and included only three individuals. A t-test performed based on the visitations of one butterfly to multiple flowers within the plot. was non-significant ($p=0.7841$, $n=17$). No butterflies visited *Eriogonum umbellatum*. Solitary bees contributed 67.5% of all visits, with flies contributing 17.5% of visits, and the remainder was made by a surphid fly. There was little difference in the percentages of visits to each of the three treatments (See Table 2).

Table 1: Number of visitations made to altered and unaltered *Linum lewissii* by all insect visitors.

	Solitary Bees	Bumble Bees	Bee Fly	Butterflies	Flies	Surphid Flies	Other Insects
Unaltered Plants	212	27	45	20	37	10	7
Altered Plants	109	17	30	7	20	9	10

Table 2: Number of visitations made to control, reduced, and enlarged *Eriogonum subalpinum* by all insect visitors.

	Solitary Bee	Fly	Bee Fly
Reduced Size	7	3	1
Control	10	5	0
Enlarged Size	10	4	0

DISCUSSION:

Relationships among butterfly morphological features:

Butterfly proboscis length, body length, and body mass were found to be significantly, positively correlated (Figure 1) in agreement with the morphological scaling found in separate studies by Knute (2007), Corbet (2000), and Boggs (1988). Such size based scaling in butterflies is consistent with morphological scaling found in other organisms as well (Borrell 2007, Agosta and Janzen 2005, Bullock 1999, Silva 1998, Bullock and Pescador 1983). These relationships are important as they are correlated to multiple life-history traits and influence the number and types of interactions which can occur within a community (Woodward et al. 2005). The longer proboscis lengths observed in larger butterflies may increase the number of flower nectaries accessible to them, providing for their greater nectar requirements as compared to smaller butterflies. This feature may also increase their generality as pollinators.

Size influences on visitation rate:

Butterfly size (as measured by both mass and proboscis length) was significantly related to visitation rate both across the floral community and within individual floral species, providing evidence in support of the second hypothesis. Butterflies of all sizes were observed to feed from the same floral species (see Appendix). However, larger individuals have higher energetic requirements than smaller individuals (Peters 1983), which for butterflies is provided by nectar from flowers. This means that larger butterflies must obtain higher quantities of nectar than smaller butterflies to maintain their metabolic processes. As they are feeding from the same floral species, more visits must be made to obtain the higher levels of nectar. The results of this

study suggest that this is occurring within the pollinator community. As larger butterflies are more frequent visitors to flowers than smaller butterflies, it is possible that their role as pollinators is more important than that of smaller butterflies as they have more opportunities to pick up pollen on their bodies and distribute it on the stigmas of more flowers. This, however, is speculation and would require further study in pollinator efficiency to determine how butterfly visitation is affecting plant reproduction from the plant's perspective.

Interestingly, floral display size did not appear to have a significant influence on visitation rate, contrary to what has frequently been reported both for butterflies and for the entire insect pollinator community in general (Gomez et al. 2008, Arroyo et al. 2007, Buide 2005, Vaughton & Ramsey 1998, Schemske 1976). This may have been due to a short observation period which failed to capture the actual visitation to large floral displays or to error in measuring the floral size actually important in influencing visitation. It is also possible that other factors are much more important in determining visitation than floral display size. Nectar depth and abundance were shown to be important factors in determining plant-butterfly interactions in concurrence with findings by Stang et al. (2006). It is also interesting that butterflies, which have some of the longest probosces of insect pollinators (Krenn et al. 2005), visited flowers with deeper nectar tubes more frequently than those with shorter nectar tubes, even though they did visit flowers with a range of nectar tube depths. This suggests that there may be more morphological matching between proboscis length and the nectar tube depth of visited flowers than previously thought. Butterflies may visit flowers with deeper nectar tubes more frequently than they do flowers with short nectar tubes due in part to competition with other insect pollinators. By visiting flowers accessible to fewer insects, the chances of obtaining

nectar are greater, potentially resulting in more energetically optimal foraging efforts, though this requires further study.

Size influences on handling times:

Neither butterfly size nor floral display size was significantly related to handling time. However, there did appear to be a negative trend between butterfly proboscis length and handling time within a plant species (Figure 5). The negative trends I observed combined with Herrera's (1989) findings that butterfly handling time decreased with increasing proboscis length as well as Inouye's (1980) study showing the same relationship with bumblebees, suggests that a relationship between the two variables likely does exist. Failure to capture this relationship was probably due to difficulty in ascertaining handling time per flower. In this study handling time was defined as the total amount of time spent on a floral head, excluding events which were clearly not feeding bouts. However, this method ignores differences based on the number of flowers a butterfly actually probes, contributing to the large variation. Determining handling time per flower rather than per floral head would be more informative and reveal if a relationship between butterfly size and handling time really does exist. This might best be done by using a video camera to record feeding bouts and counting frames or by observing single feeding bouts with binoculars, a counter, and stop watch in the field, rather than following individual butterflies to try to determine both handling time and visitation rate simultaneously.

There seemed to be no relationship between floral display size and handling time. This suggests that the energetic expenditures of maintaining a position upon a floral display are not greatly different between floral displays of various sizes. However, there are many other morphological features, such as distance between individual flowers and the spatial distribution

of nectar within a floral display which differ between the plant species which were visited. These factors were not investigated either in their influence on handling time, nor on their potential to confound the study. It is possible that looking only at species with similar nectar depths, nectar distributions, and distances between individual flowers in an inflorescence, but differing display sizes may reveal that size does have some influence on handling time, though other morphological features are more important in influencing this feature. Due to difficulties in finding species meeting these requirements, it may be more valuable to make experimental manipulations of size within one flower species (see below) or to use a species (such as *Arenaria congesta*) which naturally varies in size, to control for other confounding factors.

It is also worthy to note that exclusion of a single plant species resulted in a significant negative relationship between floral display size and handling time. This plant species, *Eriogonum subalpinum*, forms a floral display from multiple umbels. However, umbels do not align to form a continuous platform and differ in height as well. Thus, the umbel size may be more important for handling time than the total size of the display, which may imply that floral size does have an impact on butterfly handling time. Due to the incongruous results of this study, more research is needed before any conclusions should be made on the influence of floral display size on handling time.

Experimental size manipulations on handling time and visitation rate:

Butterfly visitation was too low at both experimental locations to draw any statistical conclusions on the influence of floral size on visitation. There was also no statistically significant difference between the handling time for the control and size reduced *Linum lewissii*. This is probably because the sample size (n=17) was too small to reveal any differences that may

exist. It therefore seems that either a greater amount of time on the magnitude of a multi-year experiment or locations where butterfly abundance is higher, is needed to obtain enough observations to make any conclusions. Butterfly flight paths tend to be very great, so the odds of them appearing in small plots seems to be rather small and may lead to an underestimation of the importance of butterflies as pollinators within a pollinator network.

CONCLUSION:

This study indicates that, for butterflies, body size is an important factor influencing visitation rate. It also appears to influence handling time, with increasing body size negatively related to handling time. Floral display size does not seem to be an important factor determining visitation, contrary to findings in other studies. It seems that plant abundance and nectar tube depth are much more important factors in determining visitation. The influence of floral display size on handling time is somewhat contradictory, requiring that more intensive studies on handling time be conducted before deciding how influential floral display size is on handling time. A greater understanding of factors governing these interactions is essential for forming a more comprehensive picture of the overall community, creating more accurate prediction models, and generating better conservation programs. The results provided by this study may be incorporated into such prediction models forming a more comprehensive understanding of the plant-pollinator community in a dry rocky meadow.

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APPENDIX:

All butterfly visitors and the number of visits each species (or genus/family when species is unknown) was observed to make to each flower species.

		<i>Erigeron flagellaris</i>	<i>Eriogonum umbellatum</i>	<i>Potentilla fruticosa</i>	<i>Potentilla gracilis</i>	<i>Arenaria congesta</i>	<i>Eriogonum subalpinum</i>	<i>Viguiera miliflora</i>	<i>Linum lewissii</i>	<i>Heterotheca villosa</i>	<i>Galium boreale</i>	<i>Achillea millefolium</i>	<i>Erigeron speciosus</i>	Total
	Plant Abundance	1080	880	476	310	7161	46	1586	29	10835	3146	31	1919	27499
Butterfly Species	# Individuals followed													
<i>Chlosyne acastus</i>	13	4	1	1	0	8	0	0	0	1	0	0	1	16
<i>Coenonympha tullia</i>	41	13	8	0	0	32	4	3	0	15	1	0	6	82
<i>Colias alexandra</i>	12	0	0	0	0	0	0	3	18	8	0	0	4	33
<i>Hesperiidae</i>	7	0	1	0	0	12	0	0	0	5	0	0	0	18
<i>Lycaena heteronea</i>	39	0	0	0	0	27	1	34	0	20	6	2	29	119
<i>Lycaena nivalis</i>	27	34	2	0	0	3	0	4	0	5	3	0	13	64
<i>Papilio rutulus</i>	4	0	0	0	0	13	0	0	0	0	0	0	1	14
<i>Polyommata</i>	17	7	1	0	1	6	1	0	0	20	1	3	2	42
<i>Pontia protodice</i>	2	2	0	0	0	0	0	1	0	7	0	0	22	32
<i>Speyeria</i>	29	1	0	0	0	2	0	38	0	82	1	0	17	141
Total	191	61	13	1	1	103	6	83	18	163	12	5	95	560