

Pollinator-mediated selection in *Ipomopsis aggregata*: does correlational selection explain floral phenotypes?

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## ABSTRACT

The theory of pollination syndromes is pervasive in pollination biology. Correlational selection may explain why certain flower phenotypes are selected for by certain pollinators thereby offering support for the theory of pollinations syndromes. Using potted individuals of the hummingbird-pollinated alpine wildflower *Ipomopsis aggregata*, we manipulated three floral traits (flower color, size of the nectar reward, and floral orifice shape) to generate a total of eight character combinations. Plants were set up in an artificial array in the field and pollinator visitation was observed. No significant interactions between trait combinations on the mean visitation rate per treatment per hour were found for the experiments as a whole. However, when data were analyzed separately by hour, there was a significant interaction between color and petal shape seen during the second observation hour, which affected mean visitation rate. Further experimental investigation of only two traits (size of the nectar reward and floral orifice shape) revealed a significant effect of nectar on mean visitation rate also during the second hour of observation. Our results do not provide consistent support for correlational selection.

## INTRODUCTION

Plant-pollinator interactions have long fascinated biologists. One prominent concept in pollination biology is that of pollination syndromes. Floral traits, such as color, odor, shape, and reward type can all affect the type and frequency of visitation a flower receives. It has been suggested that certain combinations of these traits are often associated with certain types of pollinators (bees, butterflies, hummingbirds, etc.); these

associations are known as pollination syndromes (Gurevitch *et al.* 2002). The idea of pollination syndromes is controversial, however, and leads to an expectation of specialization in pollination systems. Yet with temporal variation in pollinator services and overlapping geographic ranges of plants and pollinators, specialization becomes less likely and generalization seems selectively advantageous for a plant in some cases (Waser *et al.* 1996).

Natural selection of floral traits is likely mediated by pollinators and is thus partly responsible for the divergence in floral traits among angiosperms (Maad 2000). While several studies have documented pollinator-mediated selection involving floral traits (Campbell *et al.* 1991, Melendez-Ackerman *et al.* 1997), very few have examined selection favoring certain combinations of traits, also known as correlational selection. Correlational selection should favor combinations of traits whose functional effectiveness is dependent upon on each other and whose interaction is favorable for the fitness of the organism bearing the traits (Herrera 2001). Floral traits of animal-pollinated plants are ideal to study the concept of correlational selection because they are functionally linked, and certain interactions between two or more traits may be selected for by pollinators (Armbruster 1991). Indeed, Galen and Cresswell in 1991 showed that the interaction between corolla size and nectar reward size of *Polemonium viscosum* had significant effects on the average amount of time that bumblebees spend handling and probing a flower.

This field study examined the response of pollinators to combinations of manipulations of three floral traits in *Ipomopsis aggregata*. The three traits included flower color, amount of nectar reward, and one morphometric trait: floral orifice shape.

Flowers of *I. aggregata* show natural variation among these three traits, all of which may play a role in the attraction of pollinators.

In visiting *I. aggregata*, hummingbird pollinators show a strong preference for red color, which is associated with greater nectar reward (Melendez-Ackerman *et al.* 1997). The size of a nectar reward in a flower may influence the frequency and length of visitation by pollinators and may also be correlated with some morphological character, such as increased flower size. Thus it is possible for nectar foragers to learn to visit the most rewarding flowers (Cresswell & Galen 1991). It has also been demonstrated that hummingbirds make fewer insertion errors with flowers that possess a trumpeted or lipped orifice. Therefore, trumpet-shaped flowers may benefit hummingbird pollinators because the time spent at the flower and the energy costs of errors are reduced (Smith *et al.* 1996). These three traits (red color, large nectar reward, trumpet-shaped flower) are typically found together in nature in *I. aggregata*, but need to be experimentally dissociated in order to determine if correlational selection is in play. I asked: (1) if hummingbirds preferred to visit plants with their normal color, morphology, and high nectar over other combinations, and (2) if the effects of different traits have non-additive effects on visitation, which could generate correlational selection.

## MATERIALS AND METHODS

### *Study organism*

*Ipomopsis aggregata* subsp *aggregata*, commonly known as scarlet gilia, is a monocarpic wildflower located in meadows throughout the Rocky Mountains. Plants produce scarlet, trumpet-shaped flowers which are self-incompatable and produce nectar in both the male and female phases (Campbell *et al.* 1991). Common pollinators of

*Ipomopsis aggregata* include hummingbirds (*Selasphorus platycercus* and *S. rufus*) and occasionally hawkmoths (*Hyles lineata*) (Campbell *et al.* 1997).

*Experiment 1: Manipulation of flower color, size of the nectar reward, and floral orifice shape*

This study was carried out at the Rocky Mountain Biological Laboratory in the Gothic Townsite in Gunnison County, Colorado, USA during July-August 2008. Forty individual plants of *I. aggregata*, were collected from the townsite near the proposed observation site prior to observation. Individuals were then potted in plastic pots and placed in a WeatherPORT, to prevent pollinator access to the plants during non-observation hours. Manipulations were also carried out in the WeatherPORT. Floral character manipulations on the experimental flowers included three characters: amount of nectar, flower color and floral orifice shape. On each flower stalk, 1-5 flowers were experimentally manipulated.

To manipulate nectar amount, nectar was removed from all flowers, and 4 $\mu$ L of 17% sugar solution was added to half of the plants using a microsyringe. All other plants were given a 0.5  $\mu$ L addition of 17% sugar solution. Flower color was manipulated by painting the corollas white to mimic *I. tenuituba*, a congeneric species of *I. aggregata* which is discriminated against by hummingbird pollinators (Campbell *et al.* 1997). Unmanipulated individuals were painted a red color that had been closely matched to the original color as judged by a spectrometer. Hummingbirds show no preference for unpainted flowers over painted flowers (Melendez-Ackerman *et al.* 1997). To manipulate floral orifice shape, petals of individual flowers were trimmed with scissors to

remove approximately 50% of the petal. With two alternatives for each character, eight combinations of traits were produced. They are as follows:

Normal orifice shape x original color x 0.5  $\mu$ L nectar addition  
Normal orifice shape x original color x 4  $\mu$ L nectar addition  
Normal orifice shape x white color x 0.5  $\mu$ L nectar addition  
Normal orifice shape x white color x 4  $\mu$ L nectar addition  
Altered orifice shape x original color x 0.5  $\mu$ L nectar addition  
Altered orifice shape x original color x 4  $\mu$ L nectar addition  
Altered orifice shape x white color x 0.5  $\mu$ L nectar addition  
Altered orifice shape x white color x 4  $\mu$ L nectar addition

Each combination was represented by 5 individuals collected from the field.

Test individuals were randomly assigned to positions within the array. These positions were kept constant throughout the observation period so as to provide hummingbirds with the opportunity to learn the positions of the flowers and adjust their behavior accordingly. The array consisted of 40 potted plants, each with one to five open flowers. The pots were arranged in 7 rows and 6 columns, the last row consisting of only four pots. For each observation period, the array was set up near the collection site, with at least one m buffer from other *I. aggregata* in the area. This provided a large enough barrier between test individuals and naturally occurring individuals so as to clearly distinguish the two, but was close enough to attract pollinators from the larger population of *I. aggregata*. Observations were taken twice daily, weather permitting: early morning and late afternoon/dusk because hummingbirds are most active at these times. Each observation period lasted approximately two-three hours. Observations were taken from a distance of at least 2.5 m to minimize influence over pollinator activity. Individuals in the array were maintained and reused for as long as possible. Upon necessity, individuals were replaced with new plants from the field.

The mean visitation rate per flower per hour was calculated for each plant. This measure of visitation to a plant was analyzed using a 3-way analysis of variance, with factors of flower color, nectar and petal length. This analysis allowed testing of any interactions between types of traits on mean visitation rate. Data were also analyzed separately by individual hour of observation. Any changes in behavior could reflect nectar depletion over time and/or learning.

According to the theory of pollination syndromes, pollinators specialize on flowers with certain combinations of characters. If this theory is true, it was expected that significant pollinator preference for one combination of traits over all others would be observed. For *I. aggregata*, it was expected this combination would consist of red color, normal orifice shape, and large nectar reward because these traits are common in nature, and both color and reward have been shown individually to affect visitation (Melendez-Ackerman & Campbell 1998). In its most extreme form the idea of pollination syndromes predicts not only that a combination is preferred, but that it is preferred in excess of the preference expected by adding effect of individual traits. In that situation pollinator behavior would be producing correlational selection. If there is no combination of traits that is significantly preferred over others, the theory of pollination syndromes is not supported and it is likely that correlational selection does not occur.

*Experiment 2: Manipulation of the size of the nectar reward and floral orifice shape*

To test for any interaction between only the shape of the floral orifice and the size of the nectar reward, two arrays were prepared and set up in the field, similar to experiment one. Each array consisted of 16 plants: 8 with the normal orifice shape

(normal petals) and 8 with the altered orifice shape (shortened petals). (This manipulation was carried out in the same manner as in the previous experiment.) Nectar was removed from all plants using a microsyringe. Each plant in one array received a 17% sucrose nectar solution addition of 4  $\mu$ L and the plants in the other array received a 17% sucrose nectar solution addition of 0.5 $\mu$ L. With two alternatives for each of the two traits, four combinations of traits were produced: They are as follows:

Normal orifice shape x original color x 0.5  $\mu$ L nectar addition  
Normal orifice shape x original color x 4  $\mu$ L nectar addition  
Altered orifice shape x original color x 0.5  $\mu$ L nectar addition  
Altered orifice shape x original color x 4  $\mu$ L nectar addition

Individual plants were randomly assigned to positions within the array. The high and low nectar arrays were placed 10 meters apart in the field, and the positions of the arrays were switched at the beginning of each new observation day. Observations were conducted in the same manner as described in the previous experiment.

The mean visitation rate per flower per hour was calculated for each plant. In preliminary analysis, mean visitation to a plant trait was first analyzed using a split-plot ANOVA, with day as a block factor, nectar as the whole plot factor, and petal length as the split-plot factor. No nectar x day interaction was detected, suggesting that the position of the array had no effect on mean hummingbird visitation rate. Since there was no suggestion of a position effect, data were then analyzed using a 2-way ANOVA to test for significant interaction between the shape of the floral orifice and the size of the nectar reward on mean visitation rate to a plant. As before, data were also analyzed separately by individual hour of observation. Results from experiment one and experiment two were then analyzed together using an analysis of variance. All data from experiment two and data for only red-colored flowers in experiment one were used in this analysis.

## RESULTS

### *Experiment 1: Manipulation of flower color, the size of the nectar reward, and floral orifice shape*

I witnessed twenty-four foraging bouts by hummingbirds and 293 plant visits. Twenty-one of the birds were broad-tailed hummingbirds and three were rufous hummingbirds. An analysis of variance on all of the data from this experiment detected no significant effects of color, petal shape, or nectar. Similarly, the interaction of color x nectar, color x petals, and color x petals x nectar did not significantly affect mean visitation rates to plants (Table 1). The interaction of petals and nectar amount was also insignificant, but the p-value was the lowest for all of the source variables ( $df = 1, 32, F = 3.33, P = 0.0775$ ). Both red and white flowers with normal petals saw fewer visitations with the nectar addition than without. However, both red and white plants with shortened petals saw increased visitation with the addition of nectar (Figure 1). However, when data were analyzed broken up by hour, results were quite different. On average during the first hour, mean visitation rates were similar for all treatments. During the second hour, however, interesting trends were observed. For plants with normal petals, red-colored flowers were visited more than white, but for plants with shortened petals, white-colored flowers were visited more than red (Fig 2). An analysis of variance showed a significant interaction of color x petals on mean visitation rate during the second hour ( $df = 1, 32, F = 9.50, P = 0.0042$ ) (Table 2). However, red plants with normal petals and high nectar still did not have the highest visitation rate (Fig. 2). Interestingly, the hint of an interaction between petals and nectar amount was not present during the second hour when analyzed by itself.

### *Experiment 2: Manipulation of the size of the nectar reward and floral orifice shape*

I witnessed thirty-one foraging bouts by hummingbirds and 210 plants visits. Twenty-nine of the birds were broad-tailed hummingbirds and 2 of the birds were rufous hummingbirds. Mean visitation rates to different flower treatments were not significantly different; the 2-way ANOVA showed that neither the amount of nectar, the shape of the floral orifice, nor the interaction between nectar amount and floral orifice had a significant effect on mean visitation rate (Table 3). Some interesting trends were observed, however (Fig 3). For plants with flowers possessing normal petals, the visitation rate increased from 0.5 to 0.69 visits/(flower\*hour). For plants possessing shortened petals, the visitation rate increased by more than double with the addition of nectar: from 0.41 to 0.94 visits/(flower\*hour). Combined analysis of experiment one and two (using only red-color treatments from experiment one) also showed a lack of significant effects of trait interactions on mean hummingbird visitation rate (Table 4).

When data from experiment two were analyzed separately by hour, results were again quite different. During the first hour, mean visitation rates were similar for all treatments. During the second hour, visits to plants with no nectar addition greatly decreased. Overall during the second hour, plants with normal petals and the nectar addition received the most visits, followed by plants with short petals and the nectar addition (Figure 4). An analysis of variance revealed a strong effect of nectar on mean visitation rate during the second hour ( $df = 1, 28, F = 19.54, P = 0.0001$ ) (Table 5).

### DISCUSSION

The theory of pollination syndromes suggests that plants possessing certain combinations of floral traits attract certain types of pollinators. Such an idea implies

specialization between plants and pollinators, but evidence exists which suggests that some pollination systems are instead quite generalized (Waser *et al.* 1996, Feinsinger 1978). If pollination syndromes do exist, it is likely that certain floral traits in combination are more attractive or provide greater reward to the pollinator than separately. If a certain combination is sufficiently attractive, it could generate correlational selection in which the traits interact with each other in such a way that is advantageous to the fitness of the organism bearing the traits (Herrera 2001). This experiment was designed to test whether correlational selection occurs in *Ipomopsis aggregata*, which will provide some insight into the reality of pollination syndromes. Such correlational selection could be generated by patterns in pollinator visitation, as tested here, or by the integrated effects of certain traits on the efficiency of pollen transfer.

The first experiment utilized the floral traits of color, nectar reward size, and floral orifice shape to investigate if these traits are functionally linked to pollinator attraction. It was hypothesized that *I. aggregata* plants possessing red flowers, the normal floral orifice shape and a larger nectar reward would be most preferred by pollinators, and furthermore that traits would interact in their effects on visitation. However, during the experiment as a whole, the predicted combination did not receive the highest visitation rate, and no significant interactions between traits were found.

When data were analyzed on an hourly basis, significant differences in visitation rates were detected. During the first hour of observation, average visitation rates per treatment were similar, but the second hour showed an interaction between color and petals. It appeared that hummingbirds learned during the first hour of observation and

adjusted their behavior to favor white short-petaled flowers over red- short petaled flowers, and red normal-petaled flowers over white normal-petaled flowers.

Interestingly, nectar had no effect on visitation rate and equally surprising is that with individuals possessing shortened petals, white color was preferred. These findings are in disagreement with the earlier findings that hummingbirds prefer red color because it is commonly associated with a greater nectar reward (Melendez-Ackerman and Campbell 1998). One speculation as to the reason white color was preferred when petals are shortened is because in the absence of a nectar-guiding orifice shape, the unpainted interior of the floral tube may have acted as a point of orientation or guide for beak insertion, a trait which was lacking in the red flowers.

The interaction between the floral orifice shape and size of the nectar reward was the closest to significant during preliminary analysis of the first experiment, leading to a redesign of the experiment using only the treatments of petal shape and nectar addition to focus on this relationship. Again, no interactions were found between the effects of traits on mean visitation rate. Similar trends were observed between both experiments concerning plants with shortened petals. Adding nectar to plants with shortened petals increased the mean visitation rate for both red and white flowers.

When data were analyzed on an hourly basis, the second hour showed higher visitation rates for flowers (both with normal petals and shortened petals) receiving the high nectar addition. It appears that during the first hour of observation, hummingbirds were visiting all treatments indiscriminately. Due to the fact that the second hour showed such a change in hummingbird behavior, it can be supposed that the hummingbirds learned which plants were most rewarding from their first encounter and chose to re-visit

those plants. During that second hour, visitation was highest to plants with the normal petals and high nectar, but no interactions between traits were detected.

Results obtained which were in disagreement with previous study, such as the seeming lack of preference for greater nectar rewards or red color in the first experiment may be explained by the spacing of individual plants within the arrays. During the first experiment, individuals were placed in very close proximity to one another, approx. 15-20 cm apart. While the densely clustered plants may have attracted pollinators to the area, the ability of hummingbirds to distinguish between experimental treatments may have been hindered. The pots may have been too close together for the hummingbirds to remember and recognize the position of certain plants and therefore may not have been able to adjust their feeding behavior so as to visit plants which were most rewarding or attractive. In such dense groupings, plants with low nectar may have benefited by having nectar-rich neighbors even if they may have possessed floral features less attractive to pollinators. Klinkhamer and van der Lugt (2004) found that the positive effects of high nectar production rates for individual plants disappear in denser populations. The finding of a strong nectar effect in experiment two (where the high and low nectar arrays were 10 m apart) but not in experiment one is consistent with the effect of density pointed out by Klinkhamer and van der Lugt (2004).

Overall, only during the second hour of one of the experiments, were visitation rates highest to the combination predicted, normal petals and high nectar. In addition, only a hint of correlational selection was found within this particular pollination system, though results were inconsistent throughout the course of the study. Only in the first experiment with three floral trait manipulations did traits interact in a significant way to

increase pollinator attraction (color x petals). No preference was shown consistently in the two experiments by hummingbirds for any combination of the three traits, however. The individual trait of nectar did have a significant effect on mean visitation rate, but only for the second experiment involving just petal and nectar manipulations. Due to conflicting results obtained from experiments one and two, there is little support for predictions made from the theory of pollination syndromes. Even if results were consistent for this particular plant species, such tests would need to be done across many plant and pollinator species to assess the validity of preferences for combinations that are embedded in the idea of pollination syndromes. This experiment was unique in its attempt to discover potential interactions between floral traits through experimental manipulation and pollinator observation. Continuation of this type of research may yet provide adequate data to discover true instances of correlational selection in floral traits and determine if pollination syndromes are valid.

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## TABLES AND FIGURES

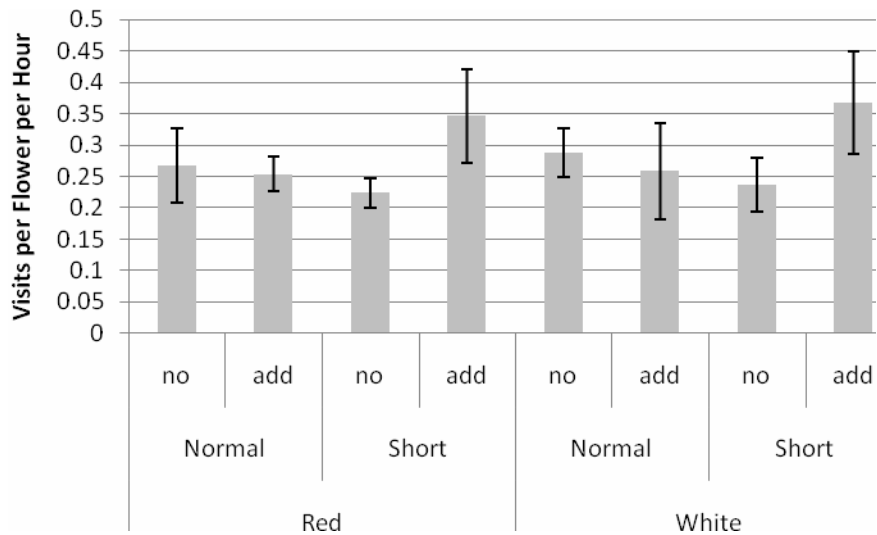


Figure 1: Mean visitation rate per treatment for experiment one. Error bars indicate 1 S.E.

Table 1. ANOVA table for effects of trait interaction on mean visitation rate per treatment for experiment one.

| Source              | df | MS      | F    | P      |
|---------------------|----|---------|------|--------|
| Color               | 1  | 0.00217 | 0.13 | 0.7195 |
| Petals              | 1  | 0.00717 | 0.43 | 0.5144 |
| Nectar              | 1  | 0.02750 | 1.67 | 0.2060 |
| Color*Petals        | 1  | 0.00005 | 0.00 | 0.9558 |
| Color*Nectar        | 1  | 0.00002 | 0.00 | 0.9693 |
| Petals*Nectar       | 1  | 0.05490 | 3.33 | 0.0775 |
| Color*Petals*Nectar | 1  | 0.00036 | 0.02 | 0.8841 |
| Error               | 32 | 0.01650 |      |        |

Table 2. ANOVA table for effects of trait interaction on mean visitation rate per treatment when data are divided by hour of observation.

| Source              | df | MS         | F    | P             |
|---------------------|----|------------|------|---------------|
| Color               | 1  | 0.00105917 | 0.05 | 0.8218        |
| Petals              | 1  | 0.00297563 | 0.14 | 0.7060        |
| Nectar              | 1  | 0.00683823 | 0.33 | 0.5680        |
| Color*Petals        | 1  | 0.19509142 | 9.50 | <b>0.0042</b> |
| Color*Nectar        | 1  | 0.01789850 | 0.87 | 0.3576        |
| Petals*Nectar       | 1  | 0.00009000 | 0.00 | 0.9476        |
| Color*Petals*Nectar | 1  | 0.00610144 | 0.30 | 0.5895        |
| Error               | 32 | 0.02054314 |      |               |

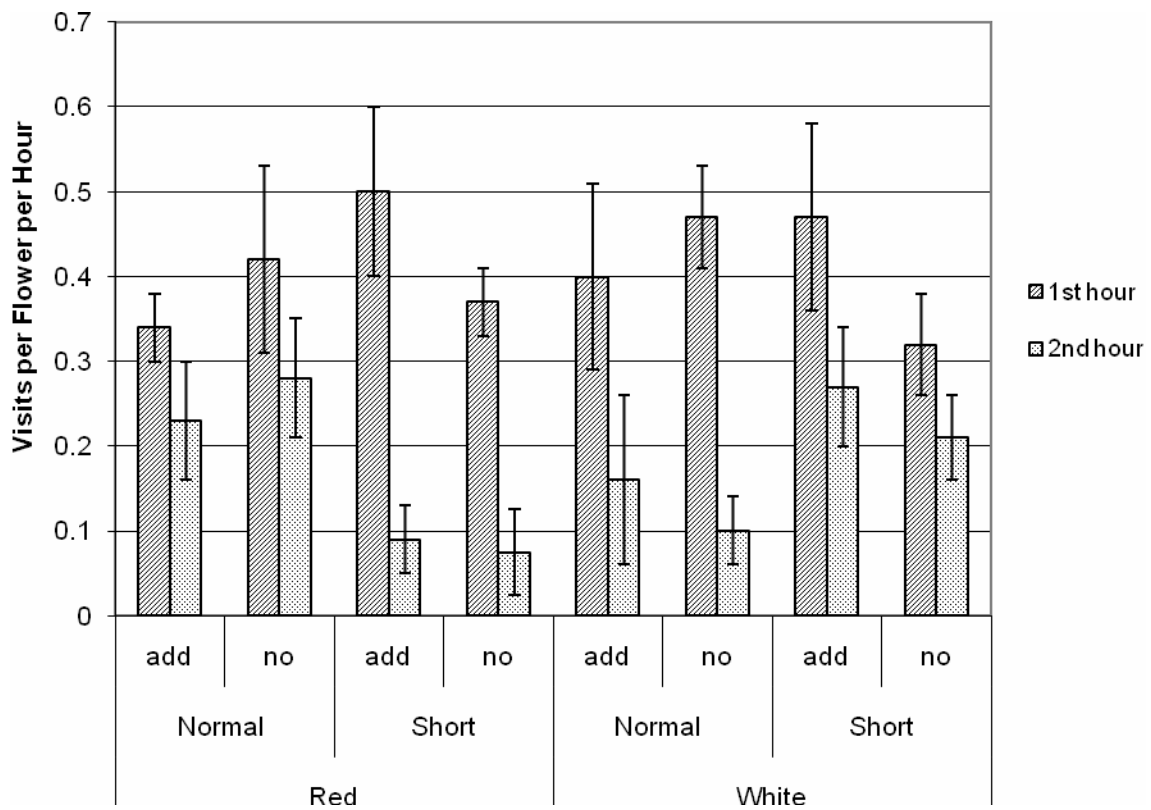


Figure 2. Mean visitation rate per treatment, separately by hour for experiment 1. Error bars indicate 1 S.E.

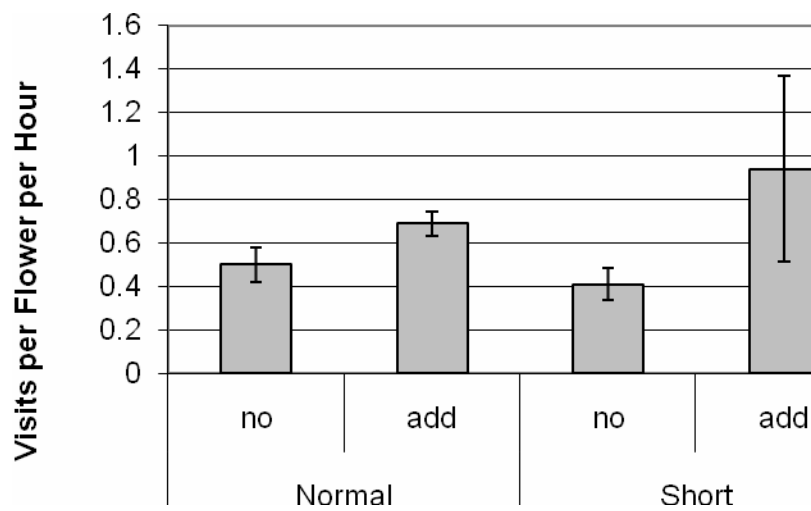


Figure 3. Mean visitation rate per treatment for experiment 2. Treatments are divided into plants with normal or short petals, with no nectar added (0.5 $\mu$ L) or with the nectar addition (4  $\mu$ L). Error bars indicate 1 S.E.

Table 3. ANOVA table for effects of trait interaction on mean visitation rate per treatment for experiment two.

| Source        | df | MS         | F    | P      |
|---------------|----|------------|------|--------|
| Nectar        | 1  | 1.05235950 | 2.69 | 0.1122 |
| Petals        | 1  | 0.04823408 | 0.12 | 0.7282 |
| Nectar*petals | 1  | 0.23846824 | 0.61 | 0.4416 |
| Error         | 28 | 0.39137212 |      |        |

Table 4. ANOVA table for effects of trait interaction on mean visitation rate per treatment hour for experiments one and two together.

| Source        | df | MS         | F    | P      |
|---------------|----|------------|------|--------|
| Experiment    | 1  | 1.62023799 | 6.62 | 0.013  |
| Petals        | 1  | 0.04255259 | 0.17 | 0.6786 |
| Nectar        | 1  | 0.77378080 | 3.16 | 0.0818 |
| Petals*nectar | 1  | 0.22805523 | 0.93 | 0.3393 |
| Error         | 47 | 0.24472703 |      |        |

Table 5. ANOVA table for effects of trait interaction on mean visitation rate when data were analyzed by hour.

| Source         | df | MS         | F     | P            |
|----------------|----|------------|-------|--------------|
| Nectar         | 1  | 0.44035202 | 19.54 | <b>0.001</b> |
| Petals         | 1  | 0.07288244 | 3.23  | 0.0829       |
| Nectar* petals | 1  | 0.01931431 | 0.86  | 0.3625       |
| Error          | 28 | 0.02253469 |       |              |

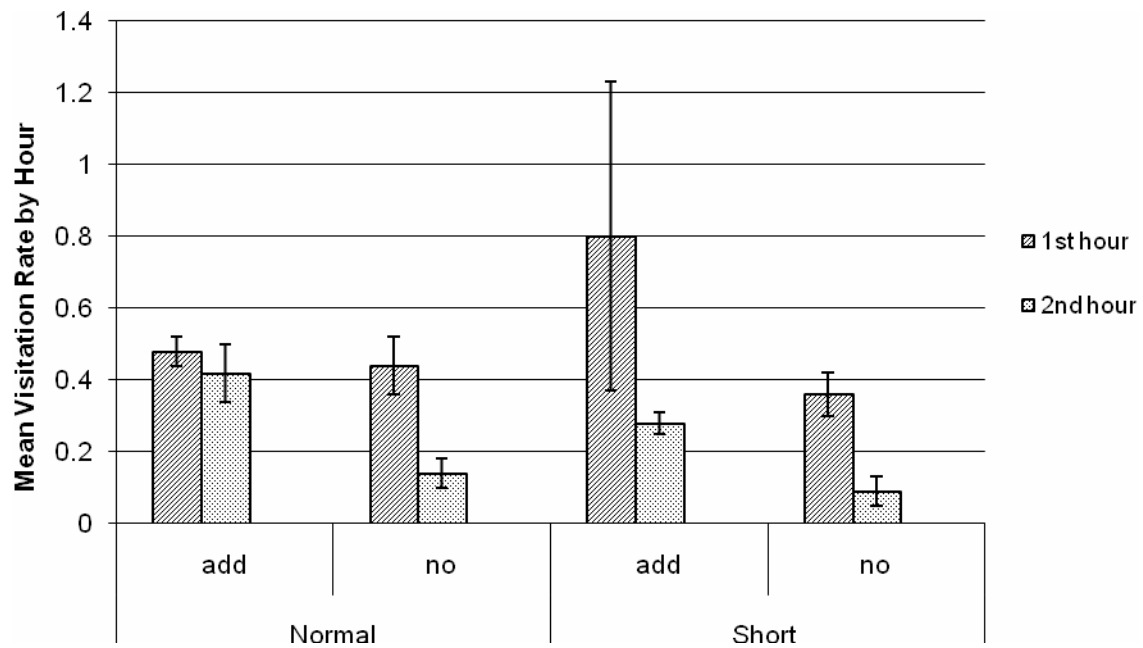


Figure 4. Mean visitation rate per treatment, separately by hour for experiment 2. Error bars indicate 1 S.E.