

Butterfly foraging behavior: Can butterflies detect nectar in flowering plants?

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Abstract:

Optimal foraging theory states that there are benefits and costs from foraging. If the animal shows optimal foraging behavior, the benefits minus the costs from foraging should be maximized. One assumption of optimal foraging theory is that animals can recognize food, which for butterflies means detecting nectar in flowering plants. We tested whether butterflies detect nectar in the field when they are foraging, or if they forage randomly until they find rewarding florets. We exposed each *Speyeria mormonia* male butterfly to a *Pyrrocoma crocea* flowerhead that was half nectar rich and half nectar poor. We recorded which side of the flowerhead the butterfly probed first and whether or not it continued probing after finding or not finding a reward. The results demonstrated that this species can detect which side of the flowerhead possesses nectar. The estimated number and proportion of nectar rich florets in the nectar rich side did not differ for individuals choosing the nectar-rich or nectar-poor side, which means individuals choosing the nectar-poor side were not doing so because of low nectar content in general. Even though *S. mormonia* males showed optimal foraging behavior by detecting rewarding florets, they did not use information about rewarding florets in the decision as to whether to keep probing the flower or not. *S. mormonia* thus lose time and energy probing unrewarding flowers. Further studies with *S. mormonia* males and females are needed to determine the mechanisms that enable their nectar detecting abilities and whether there are foraging differences related to sex.

Keywords: butterfly pollination, nectar detection, optimal foraging, *Pyrrocoma crocea*, *Speyeria mormonia*

Introduction:

Butterflies and flowering plants have a mutualistic relationship. Plants benefit from visitation by butterflies through butterfly pollination. Even though butterflies visit fewer flower heads than bumblebees, they fly significantly greater distances than other insect pollinators, which helps in plant gene dispersal by expanding the area of plant neighborhoods within a population and increasing individual plant fitness (Schmitt, 1980). Butterflies, in turn, depend on flowers since many butterfly species feed primarily on nectar (Scott, 1986). Nectar availability influences butterfly fitness by determining the number of eggs laid in some species (Boggs and Ross, 1993). As a result, flower availability per individual butterfly is one factor controlling population size in the next year for *Speyeria mormonia* and possibly other butterfly species (Boggs and Inouye, unpubl). Therefore, maximizing nectar intake through optimal foraging would greatly benefit individual butterflies.

Optimal foraging theory states that there are benefits and costs from foraging. As a benefit from feeding, animals gain food, which for butterflies means sugar, and food provides energy. Nevertheless, by foraging, they also spend time and energy looking for food and expose themselves to predators. If the animal shows optimal foraging behavior, the benefits minus the costs from foraging should be maximized (Krebs and Davies, 1984). If butterflies are optimal foragers, they should be able to maximize the difference between the benefits and costs of foraging by detecting nectar. Optimal foraging, as opposed to foraging randomly, yields more nectar per unit time or unit effort. If butterflies do not detect nectar, they cannot maximize energy intake because they will not recognize where the food is.

There are different mechanisms used by plants to attract pollinators: scent, color, humidity, and shape, among others (Goulson et al. 1998). Research has demonstrated that the

nectar scent of some flowers helps attract pollinators by communicating the location, quality, and abundance of nectar and pollen (Raguso, 2004). Some nectar and pollen foraging insects use this scent to discriminate against un-rewarding flowers, which reduces the time and energy they spend looking for food (Raguso, 2004). Nevertheless, scented nectar, or any other mechanism of pollination attraction, is dependent on the insect's ability to recognize it and respond to it (Raguso, 2004).

Most of the research that has been conducted on nectar detection has been with bumblebees, honeybees and hummingbirds. Both honeybees and bumblebees detect nectar scent after getting close to the flower, and use this ability to discriminate against un-rewarding flowers (Goulson et al. 1998). In the laboratory, many butterflies are more likely to feed from artificial flowers with scented honey than from sugar solutions (Raguso, 2004). This may indicate that butterflies have some nectar detection abilities, probably mediated by nectar scent. In adult butterflies, the antennae are the major scent sensory organ (Scott, 1986). However, some species possess olfactory organs, especially on the palpi, which are located on each side of the proboscis, and on the wing bases (Scott, 1986).

In this study, we used one butterfly species (*Speyeria mormonia*) to test whether butterflies detect nectar in the field when they are foraging, or if they forage randomly until they find rewarding florets. We predicted that butterflies would detect nectar-rich florets and visit them more often than non-rewarding florets. We measured the number and proportion of florets with nectar in each flower to test if differences in nectar quantity influence nectar detection abilities. We also asked whether butterflies are likely to continue probing the flowerhead if they find a reward or not. Based on optimal foraging theory, we expected that if butterflies find nectar

rewards, they continue probing the same flower in search of nectar, while if they don't find a reward, they fly away to another flower.

Methods:

The organisms used in this study are male *Speyeria mormonia* (Nymphalidae) butterflies, which fly from mid-July to early September in high and middle elevation mountain meadows (Pyle, 1998). *S. mormonia* feed primarily on nectar from flowering plants, and their egg production depends on nectar intake (Boggs and Ross, 1993). *Pyrrocoma crocea* (Asteraceae) was used to test the foraging behavior of *S. mormonia* because these butterflies regularly feed from this plant's flowers early in the butterfly flight season. The large size of its florets relative to other Asteraceae is beneficial to the manipulation of nectar volume and to observe into which floret the butterflies probe their proboscis.

The study was conducted during July 2008 near the Rocky Mountain Biological Laboratory in Gothic, Gunnison County, Colorado, USA. A large patch of *P. crocea* on the Kettle Ponds Road was used.

During July 17-Aug 1, 2008, we collected 48 *S. mormonia* males in the Kettle Ponds Road and the Gothic Townsite. Males were used because females fly late in the season (beginning of August). Males were kept overnight in glassine envelopes inside band-aid boxes at room temperature in the laboratory, to build up their appetite. Occasionally, due to inappropriate weather for field work, butterflies were kept for more than one night in the laboratory, in which cases they were placed in the refrigerator and fed with honey water once a day.

Each *P. crocea* flowerhead was enclosed overnight with fine netting to allow accumulation of nectar (Goulson et al. 1998), one flower per butterfly. The next day, a line was

drawn through the middle of the flowerhead, and the total number of florets on each side was counted. The nectar from the florets on one side of the flowerhead was removed with filter paper strips, and the number of florets that contained nectar out of the total number on that side was recorded. This way, each flower had nectar in half of its florets, and the other half was empty.

Each butterfly was placed on a flowerhead, exactly on the mid-line between the two treatments, inside a 30 cm diameter x 50 cm high wire mesh cage. The side with nectar removal was alternated between the left and right side of the flowerhead in relation to the butterfly head. We recorded on which side the butterfly probed with its proboscis first, whether to florets with or without nectar. We also documented whether butterflies continued to probe the other side of the flowerhead when they found or didn't find nectar in the first side they probed.

We performed a Goldstein's exact binomial (x^*) test to determine whether *S. mormonia* males detected which side of the flowerhead possessed nectar. The expected ratio was 1:1. We performed a t-test to determine whether the mean number or proportion of florets with nectar affected side choice. Finally, a Goldstein's exact binomial (x^*) test determined whether the butterflies continue probing the whole flower at random, using an expected ratio of 1:1.

Results

Male *S. mormonia* chose the nectar-rich side of *P. crocea* flowerheads significantly more often than expected (33:15 observed vs. 24:24 expected, Goldstein's exact binomial test: $x^*=2.598$, $P<0.005$; Fig 1). This indicates that this species can detect which side of the flowerhead possesses nectar. For the 33 butterflies that detected nectar, the position of the nectar rich side (left or right relative to their head) did not significantly influence their side choice (Goldstein's exact binomial test: $x^*=0.632$, N.S.; Fig 2). The same applied for the 15 butterflies

that did not detect nectar (Goldstein's exact binomial test: $x^*=0.937$, N.S.; Fig 3). Therefore, possible experimental bias, induced for example by handedness of the investigator, did not influence choice.

The number of florets that initially had nectar in the nectar poor side when nectar was removed was used to estimate the number of florets in the rich side that possessed nectar. The mean estimated number of florets with nectar on the nectar rich side was not significantly different for flowerheads on which males chose the nectar-rich vs. the nectar-poor side (Two-sample t-test: $t=0.8893$, $df=46$, N.S.; Fig 4). In the same manner, the proportion of nectar rich florets on the nectar rich side was calculated and the means did not differ between flowerheads for which males chose the nectar-rich vs. nectar-poor side (Two-sample t-test: $t=1.4054$, $df=46$, N.S.; Fig 5). Hence, the amount of nectar that had accumulated overnight in the flowerhead did not affect choice.

After finding a reward by probing the nectar rich side first, the butterflies were neither more likely nor less likely to continue to the other side of the flowerhead (Goldstein's exact binomial test: $x^*=0.174$, N.S.; Fig 6). For the butterflies that probed the nectar poor side first, continuance to the other side of the flowerhead was also random (Goldstein's exact binomial test: $x^*=0.258$, N.S.; Fig 7). Therefore, in *S. mormonia* males, there is equal probability of continuing to probe the rest of the flowerhead after finding or not finding a reward.

Discussion:

The data presented in this study support optimal foraging behavior in one species of butterfly (*S. mormonia*). By possessing nectar detection abilities, this species reduces the energy and time spent probing unrewarding flowers, leaving more time and energy for reproduction, and thereby increasing fitness (Krebs and Davies, 1984). For *S. mormonia*, the amount of nectar eaten is directly related to egg production (Boggs and Ross, 1993), which highlights the importance of effective foraging behavior in this species. Further studies with both sexes of other butterfly species would be useful to determine the extent of this behavior in butterflies.

The estimated number and proportion of florets with nectar in the nectar rich side did not explain “mistakes” in nectar detection in *S. mormonia*. This suggests that any threshold in nectar presence required for nectar detection was not reached in the present study. However, it leaves open the question of why those butterflies that chose the nectar-poor side did so.

Andersson (2003) demonstrated that butterfly species differ in their relative use of floral scent and color to recognize nectar in flowering plants, but that overall, olfactory signals are most important during foraging. Also, she demonstrated that several butterfly species recognize by scent and prefer feeding from nectar with benzenoid compounds, monoterpenes and irregular terpenes, rather than sesquiterpenes and fatty acid derivatives which had a different smell (Andersson, 2003). This indicates that several species of butterflies use their olfactory abilities to discriminate against un-rewarding flowers, since floral scent is crucial to flower selection (Andersson 2003). It is likely that *S. mormonia* also use scent, given these results, but this needs to be confirmed.

Whether or not *S. mormonia* continued probing the same flower after finding a reward was random, which indicates that they do not use information from current feeding on a

flowerhead to decide whether to continue feeding. Bumblebees, on the contrary, leave unrewarding patches of flowers and spend more time in patches with a high reward (Goulson et al. 1998). Butterflies thus are not very advanced optimal foragers, because they lose time and energy probing more flowers than it is necessary.

This study yields a simple but important discovery for butterfly pollination. *S. mormonia* meets one of the assumptions of optimal foraging theory- the ability to accurately identify food. It is still not known if this behavior applies to all species of butterflies, which is why this study serves as a beginning to many future research studies in this field.

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Figure Legends:

Figure 1. Frequency of side choice by 48 *S. mormonia* male butterflies in manipulated *P. crocea* flowerheads. One random side of the flowerhead was nectar rich and one was nectar poor. Comparison between expected percentage (50%) and observed percentage (68%).

Figure 2. For those 33 *S. mormonia* male butterflies that detected nectar by probing the nectar rich side first, the number of times that the nectar rich side was in the left or the right of the *P. crocea* flowerhead, relative to the butterfly head. Comparison between expected percentage (52%) and observed percentage (58%).

Figure 3. For those 15 *S. mormonia* male butterflies that did not detect nectar by probing the nectar poor side first, the number of times that the nectar rich side was in the left or the right of the *P. crocea* flowerhead, relative to the butterfly head. Comparison between expected percentage (48%) and observed percentage (60%).

Figure 4. Comparison between the means of the estimated number of florets with nectar on the nectar rich side for the butterflies that chose the nectar poor or nectar rich side (standard error included).

Figure 5. Comparison between the means of the proportion of florets with nectar on the nectar rich side for the butterflies that chose the nectar poor or nectar rich side (standard error included).

Figure 6. The frequency of continuance to the other side of the flowerhead for the 33 *S. mormonia* that detected nectar. Comparison between the expected percentage (50%) and the observed percentage (52%).

Figure 7. The frequency of continuance to the other side of the flowerhead for the 15 *S. mormonia* that didn't detect nectar. Comparison between the expected percentage (50%) and the observed percentage (53%).

Figure 1

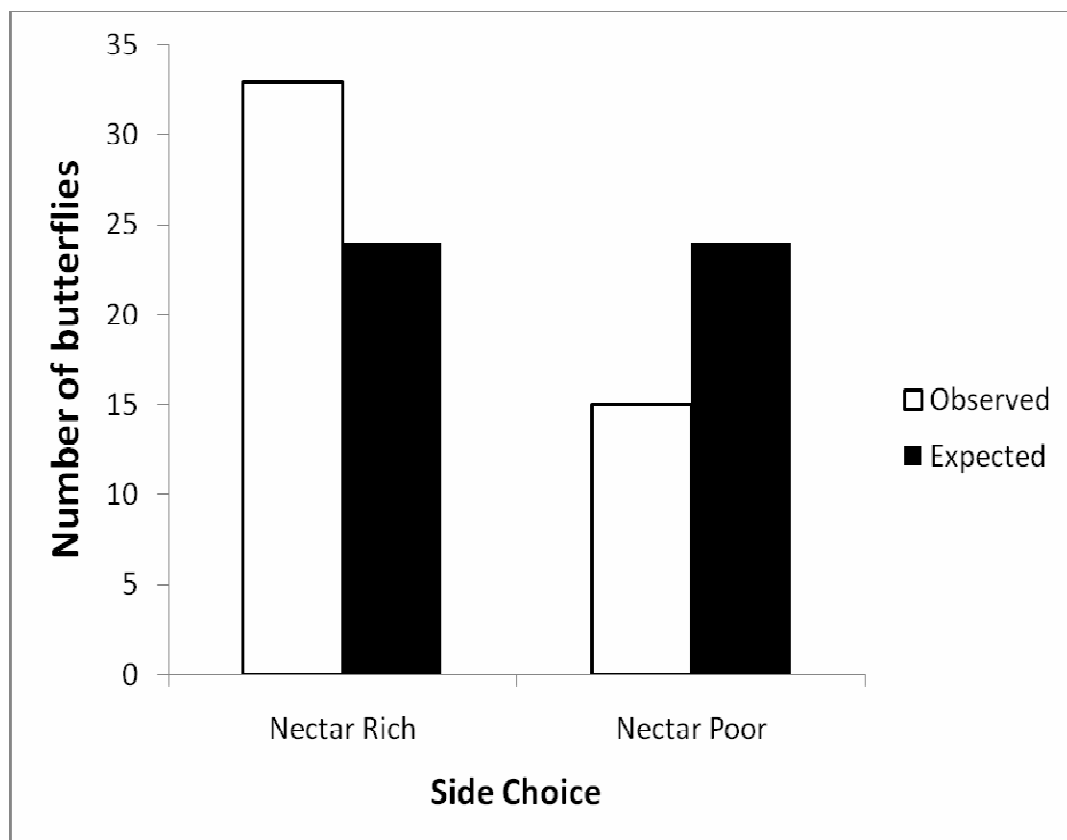


Figure 2

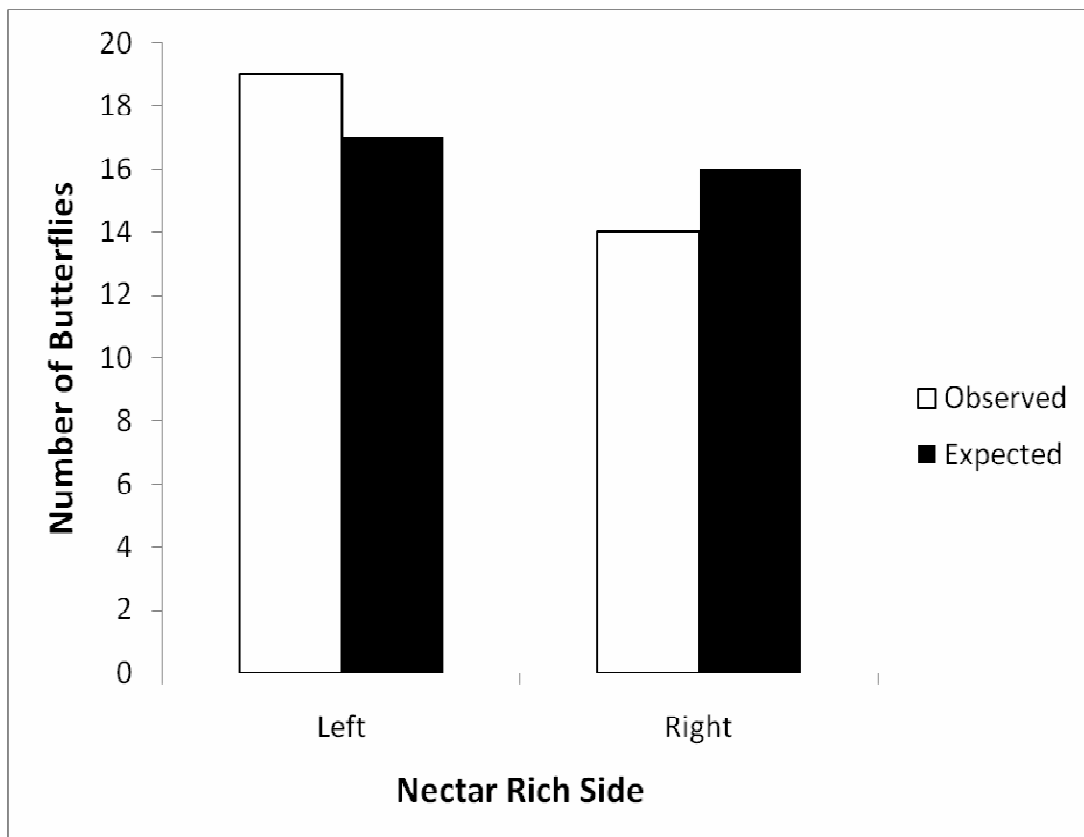


Figure 3

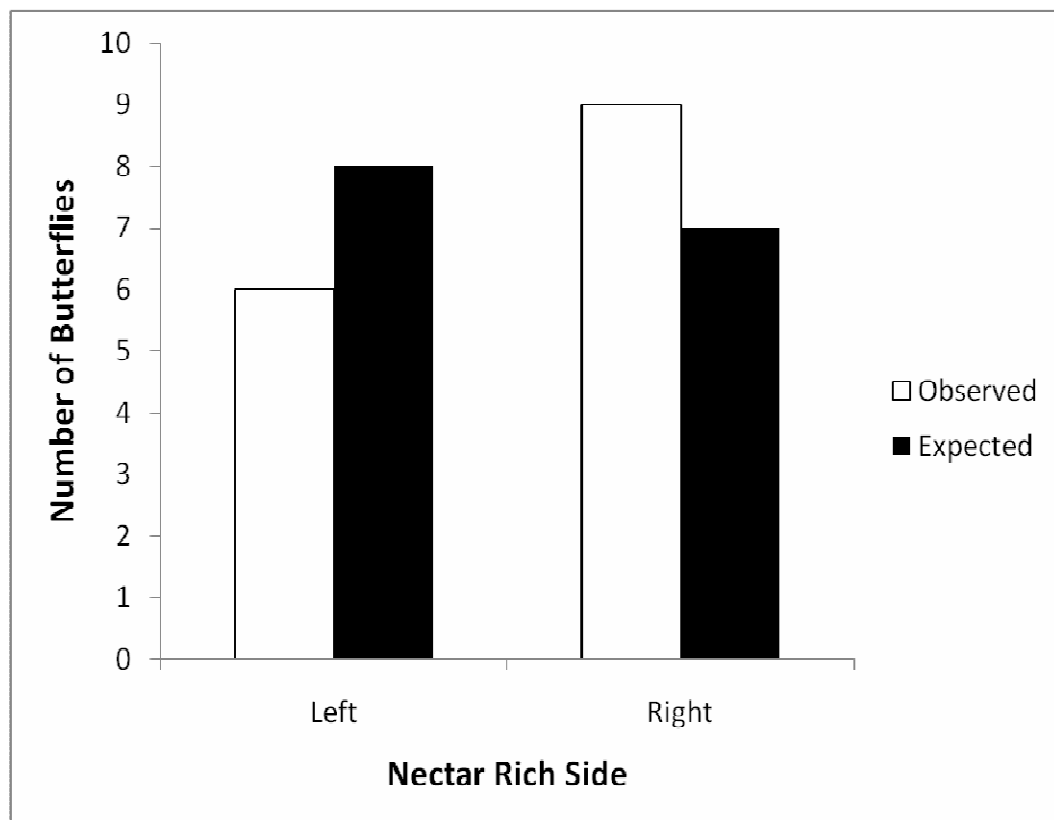


Figure 4

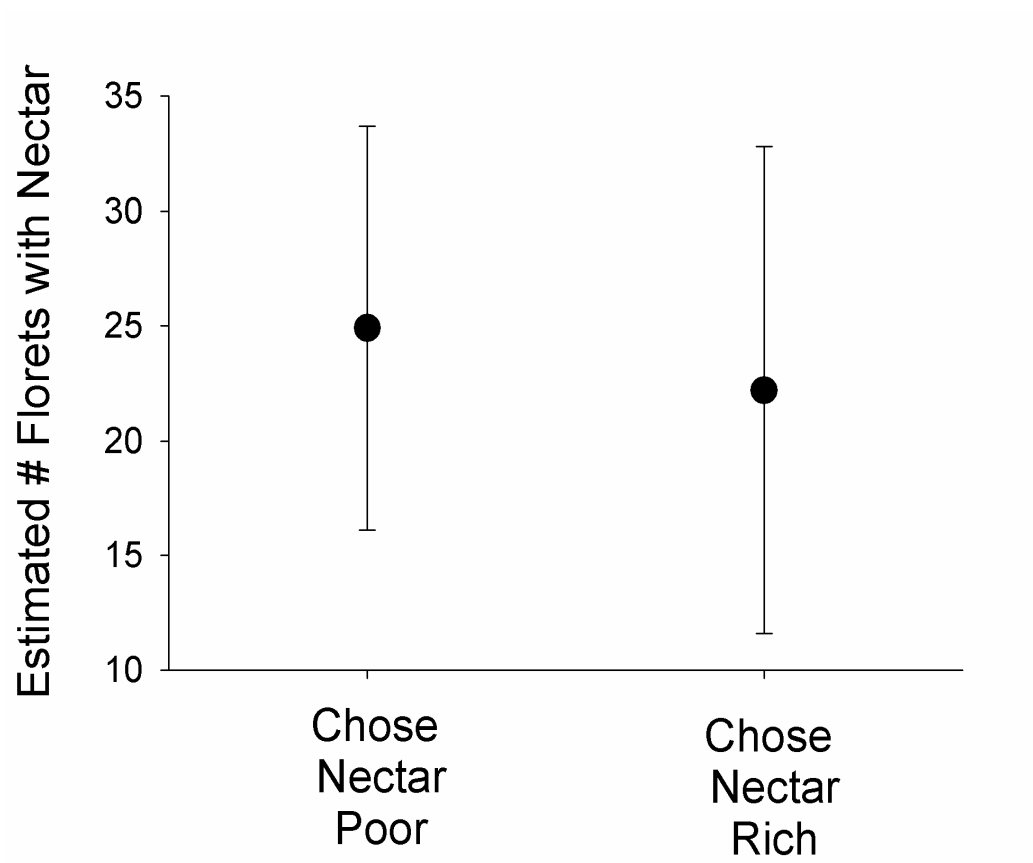


Figure 5

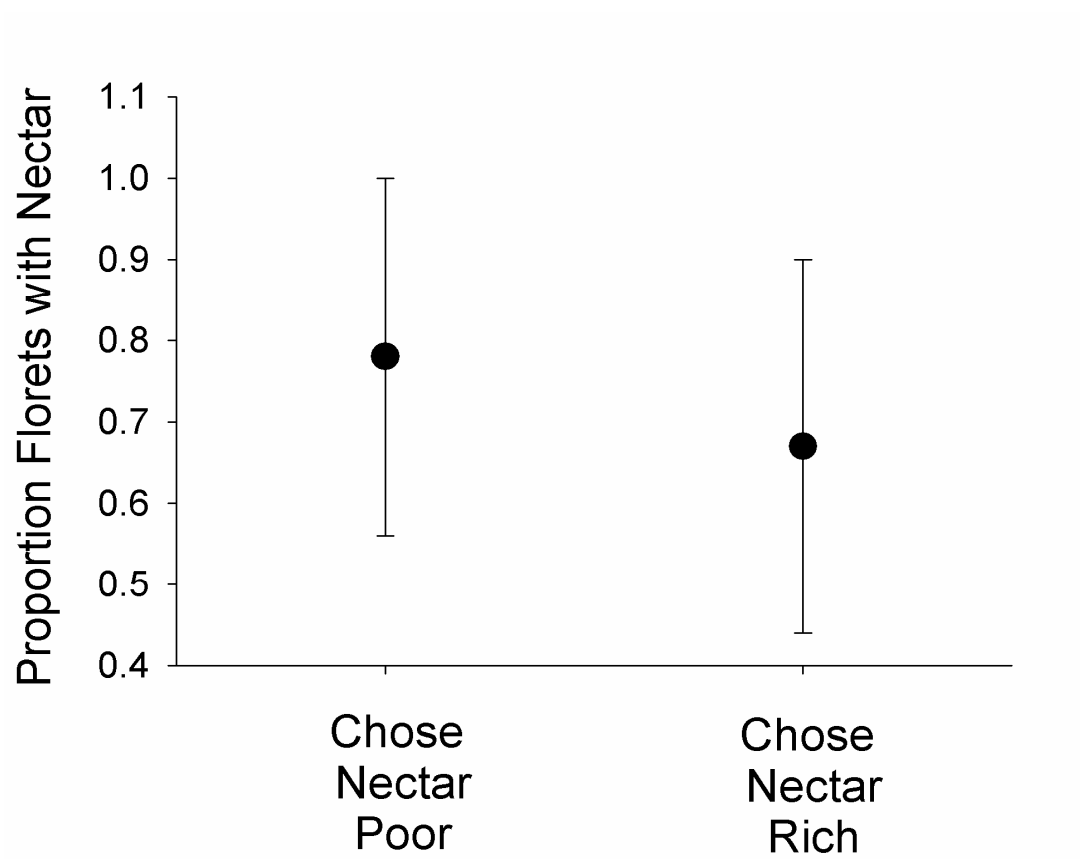


Figure 6

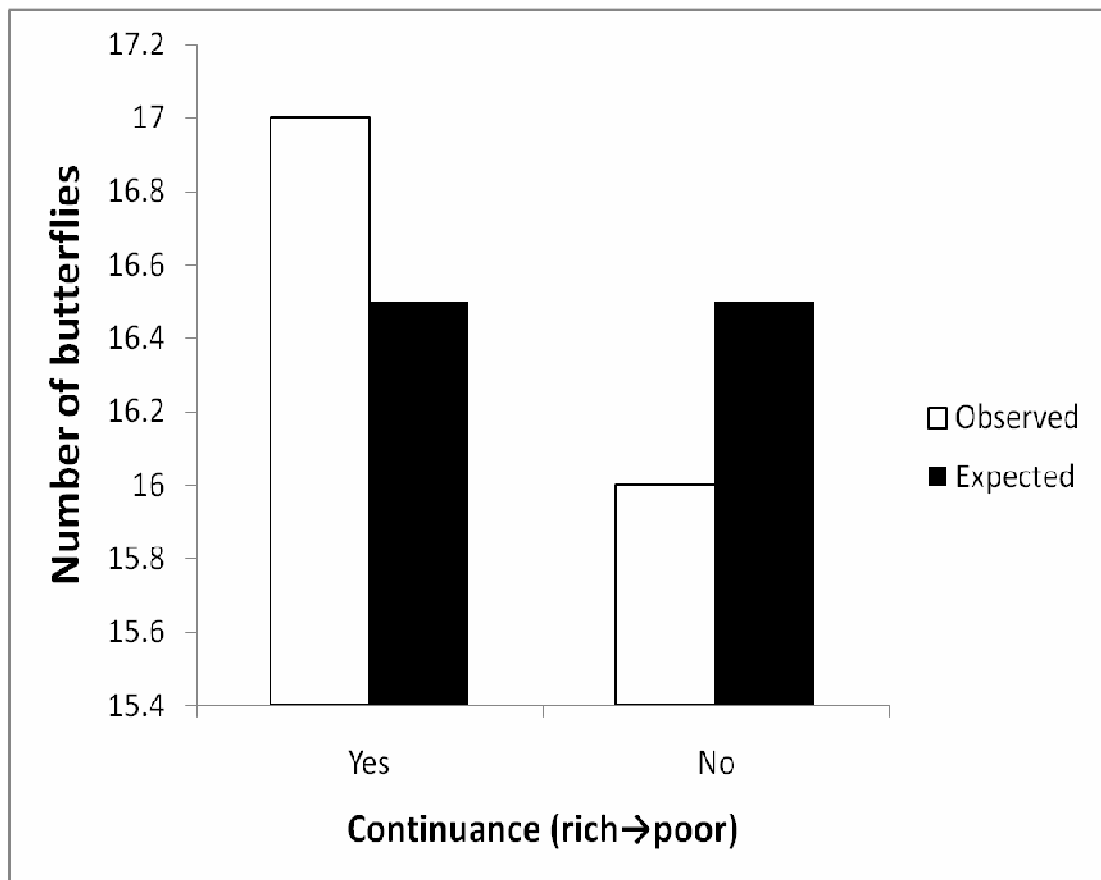


Figure 7

