

BUMBLEBEE FORAGING ON VERTICAL INFLORESCENCES:
OPTIMAL OR NOT?

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ABSTRACT

Previous studies by Pyke *et al.* have shown that bumblebees exhibit behavior that is consistent with optimal foraging theory. In this most recent effort, bumblebees were observed foraging on vertical inflorescences and their behavior was compared to a predicted model that would result in a maximum net energy gain as prescribed by optimal foraging theory. The effect of time spent on a flower and a bee's decision to remain on that inflorescence and bumblebee species distribution across patches of plants were also assessed. Contrary to what was expected, the bumblebees did not behave in a way that could be compared to the expected model. Also, no relationship was found between time spent on a flower and departure behavior. Distribution across patches of multiple species did not result in equal net energy gain for each bee species. It was concluded that the use of optimal foraging theory may not be the most complete way to describe bumblebee foraging behavior.

INTRODUCTION

Various studies of animal foraging behavior have led to the development of a concept known as optimal foraging theory, which is viewed as an attempt to explain and predict foraging behavior (reviewed in Pyke *et al.* 1977; Pyke 1984). Optimal foraging has been described as a process involving choosing a currency such as energy, determining the cost-benefit functions or establishing the constraints, and subsequently solving for the optimum that will, for example, result in a maximum net energy intake. Understanding this, an observer should be able to predict a forager's behavior under most circumstances.

Bumblebees have high energetic costs, where non-flight activities such as manipulating flowers cost 50 calories/gram/hour (Heinrich and Raven 1972; Pyke 1980) and flying costs 375 cal/g/hr (Heinrich 1975; Pyke 1980), so to be successful they must take in the most calories possible per flight. As a result, in the case of foraging bumblebees, the appropriate currency of fitness is the net rate of energy intake while foraging. Previous studies have shown that bumble bees exhibit behavior that appears to be optimal (e.g. Pyke 1978). An aim of this study was to further clarify these findings.

Previous observations of bumblebees foraging on vertical inflorescences have found that bees initiate foraging at the bottom of inflorescences and work their way up to the nearest flower, often skipping some flowers on the inflorescence and departing before reaching the top (Pyke 1978). This appears to be consistent with optimal foraging theory because the bees' movement patterns resulted in the greatest net energy intake for the

inflorescence by beginning with low flowers, which contain the most nectar, and departing before reaching the top flowers, which would most likely contain little to no nectar. Moving to the nearest flower would save time relative to moving to the next higher flower and is therefore also consistent with optimal foraging. Further investigations are required, however, to determine if the bees' foraging on them as observed is resulting in the maximum net energy gain possible.

Foraging bumblebees must constantly make decisions about whether to stay at a particular location or relocate that result in patterns and behaviors regarding how the bees forage on inflorescences (Pyke 1978). In this study it was assumed that bees collecting nectar would choose to leave an inflorescence and move to another based on nectar thresholds corresponding to each flower visited. Once the distribution of nectar in inflorescences and the amounts of nectar obtained from each flower by bees was determined, an array of potential thresholds was evaluated, the optimal threshold determined, and bee behavior predicted. From this, the motives behind bumblebee decision-making were interpreted in a different light and expectations for how many flowers a bee would visit per inflorescence were derived. It was expected, furthermore, that the amount of time spent by a bumblebee at a flower would increase with increasing nectar volume obtained at the flower. Hence, under the optimality hypothesis, it was also expected that the likelihood of a bumblebee visiting another flower on its present inflorescence would increase with the amount of time spent at the last flower.

To date, few examinations have been made of the distribution of bumblebee species across patches of plants, and another aim of this study was to determine whether or not bumblebees are distributed across patches of plants in a way that achieves equal net energy gain in accordance with 'ideal free distribution' (Fretwell and Lucas 1970). An 'ideal free distribution' would occur when the net rates of energy intake for bumblebees in nearby patches of plants are equal and is expected under the hypothesis that bumblebees are foraging in ways that maximize their net rates of energy intake (Fretwell and Lucas 1970). Furthermore, it was expected that conspecifics foraging on different species of plants would differ in size due to the differing corolla lengths of the plants.

The purpose of this study was multifold. First, nectar availability in three plant species with flowers that grow in vertical inflorescences, *Delphinium nuttallianum*,

Delphinium barbeyi, and *Aconitum columbianum*, and bees' caloric needs were used to predict foraging behavior based on an array of possible nectar thresholds bees may employ to achieve a maximum net energy gain in accordance with optimal foraging theory. The theoretical behavior was then compared to the observed to assess the success of the model. Second, the times spent on flowers were compared to a foraging bee's decision to stay on a particular inflorescence or relocate to a new one. Finally, bumblebee distribution across patches containing more than one species of the target plants was assessed to verify whether the bee species were distributed in such a way that they achieved equal net energy gain.

METHODS

This study was conducted in the vicinity of the Rocky Mountain Biological Laboratory in Gothic, CO (elevation = 2900 m). Five separate locations covering areas with 25 m radii were chosen based on abundance of the target plant species. The first three sites contained abundant *Delphinium nuttallianum* and the other two contained both *Delphinium barbeyi* and *Aconitum columbianum* growing together. Data pertaining to *D. nuttallianum* were collected between 26 June 2009 and 7 July 2009. *Delphinium barbeyi* and *A. columbianum* have a later growing season than *D. nuttallianum* does, so data pertaining to these species were collected between 7 July 2009 and 1 August 2009.

The distribution of nectar across 60 inflorescences of *D. nuttallianum* was measured using 1 mm filter paper wicks. The wicks had been calibrated using known volumes of water. Nectar volume, flower position, and corolla length were recorded for each flower on each inflorescence. Sugar concentrations in an additional sample of 10 flowers chosen at random were determined using a field refractometer.

These methods were also used to determine the distribution of nectar across 50 inflorescences each of *D. barbeyi* and *A. columbianum*. Sugar concentrations in 20 flowers each of both species were also found using the same methods employed with *D. nuttallianum*.

Ten individuals each of the most common bumblebee species and castes to visit the target plants were caught while foraging on them. These were *B. appositus* queens and workers and *B. flavifrons* workers. The bees were chilled to reduce movement and

their masses, body lengths, and thorax widths were determined. Using this method it was not possible to measure proboscis lengths directly, so these lengths were estimated using previously known values (Inouye 1980, Pyke 1982).

A digital video camera was used to record *B. appositus* queens and workers and *B. flavifrons* workers foraging on inflorescences of *D. nuttallianum*, *D. barbeyi*, and *A. columbianum*. The footage was used to determine the average times spent on flowers, flying between flowers on the same inflorescence, and flying between inflorescences. The footage was also used to compare times spent on a flower to a bee's decision to stay on an inflorescence or leave in favor of a new one.

These times, the average masses of the bees, and the nectar volumes obtained from flowers were used to develop an optimal foraging model based on nectar thresholds that would yield a maximum net energy gain. To do this, thresholds of 0.5, 1.0, and 2.0 μL of nectar were set as baseline volumes a bee might be searching for. The theoretical bee was then moved through each inflorescence beginning at the lowest flower of each. If nectar amounting to at least the threshold was found, the bee remained on that inflorescence and moved to the next lowest flower. If nectar less than the threshold amount was found the bee left that inflorescence and moved to the lowest flower of the next. After each inflorescence in the data set had been visited, the amount of nectar gained per threshold, the number of flowers visited, the number of flights made within an inflorescence, and the number of flights made between inflorescences were determined. Using the average times spent to complete these activities from the video footage and the average masses of the bees, the net rate of energy intake per second was calculated for each threshold. The frequency distribution of flowers visited per inflorescence using the various thresholds was then compared to the observed behavior from the video footage.

RESULTS

Sugar concentration was similar among the plant species, ranging only from 39.60% sugar in *Delphinium barbeyi* to 43.90% sugar in *Aconitum columbianum* (Table 1). These differences were not found to be statistically significant (ANOVA, $p=0.17$)

<i>Species</i>	<i>Mean sugar concentration (%)</i>	<i>Standard error mean</i>	<i>No. flowers</i>
<i>D. nuttallianum</i>	42.20	1.22	10
<i>D. barbeyi</i>	39.60	1.68	20
<i>A. columbianum</i>	43.90	1.77	20

Table 1: Mean sugar concentration per plant species.

Sizes of bees varied among the species and castes (Table 2), where *Bombus flavifrons* workers had an average mass of 99.00 mg and *B. appositus* workers ranged in average mass from 172.09 mg to 208.78 mg. *Bombus appositus* queens had an average mass of 560.36 mg. A one-way ANOVA showed that the differences between the masses of *B. appositus* workers foraging on *D. barbeyi* and *A. columbianum* were significant ($p=0.03$). The differences between thorax widths were found not to be significant ($p>0.14$).

<i>Species</i>	<i>Caste</i>	<i>No. bees</i>	<i>Foraging on</i>	<i>Mean mass (mg)</i>	<i>Standard error mean</i>	<i>Mean thorax width (mm)</i>	<i>Standard error mean</i>	<i>Proboscis length estimate (mm)</i>
<i>B. appositus</i>	queen	10	<i>D. barbeyi</i>	560.36	32.58	9.00	0.49	12.8
<i>B. appositus</i>	worker	10	<i>D. barbeyi</i>	208.78	17.10	6.20	0.82	10.5
<i>B. appositus</i>	worker	10	<i>A. columbianum</i>	172.09	12.77	5.60	0.23	10.5
<i>B. flavifrons</i>	worker	10	<i>A. columbianum</i>	99.00	5.75	5.050	0.22	7.3

Table 2: Mean masses, thorax widths, and proboscis length estimates for each bumblebee species studied. Note that *B. appositus* queens were caught while foraging on *D. barbeyi*, however, these values were only used in calculations pertaining to *D. nuttallianum*. *B. appositus* workers were used in calculations pertaining to *D. barbeyi*.

<i>Plant species</i>	<i>Bee species</i>	<i>Caste</i>	<i>Mean time spent on a flower (seconds)</i>	<i>Standard error mean</i>	<i>Mean time spent on intra-infl. flights (s)</i>	<i>Standard error mean</i>	<i>Mean time spent on inter-infl. flights (s)</i>	<i>Standard error mean</i>
<i>D. nuttallianum</i>	<i>B. appositus</i>	queen	1.34	0.12	0.52	0.032	1.27	0.11
<i>D. barbeyi</i>	<i>B. appositus</i>	worker	2.90	0.24	0.97	0.091	1.90	0.13
<i>A. columbianum</i>	<i>B. appositus</i>	worker	4.45	0.46	1.19	0.13	1.80	0.16
<i>A. columbianum</i>	<i>B. flavifrons</i>	worker	4.13	0.48	1.22	0.14	2.11	0.13

Table 3: Mean times for all foraging activities for 35 replicates each.

A threshold of 1.0 uL of nectar was found to result in the most calories gained per second for each plant and bee species (Table 4, Figure 1).

<i>Plant species</i>	<i>Bee species</i>	<i>Caste</i>	<i>0.5 uL threshold</i>	<i>1.0 uL threshold</i>	<i>2.0 uL threshold</i>
<i>D. nuttallianum</i>	<i>B. appositus</i>	queen	0.145 cal/sec	0.156 cal/sec	0.130 cal/sec
<i>D. barbeyi</i>	<i>B. appositus</i>	worker	0.182 cal/sec	0.206 cal/sec	0.177 cal/sec
<i>A. columbianum</i>	<i>B. appositus</i>	worker	0.0520 cal/sec	0.0593 cal/sec	0.0350 cal/sec
<i>A. columbianum</i>	<i>B. flavifrons</i>	worker	0.0553 cal/sec	0.0623 cal/sec	0.0376 cal/sec

Table 4: Theoretical net rates of energy gain per second for each plant and bee species.

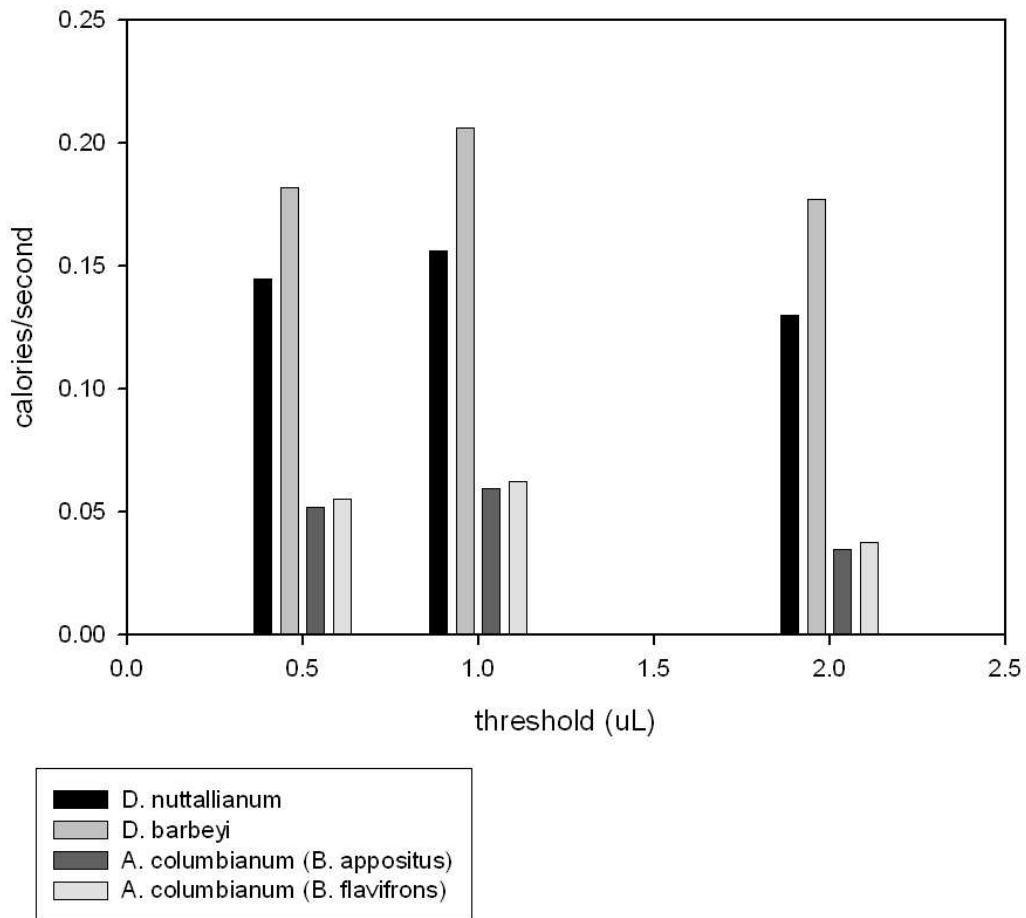


Figure 1: Theoretical rates of net energy gain per plant species and nectar threshold.

The times spent on flowers of any species were found not to significantly affect a foraging bee's decision to stay on an inflorescence or leave, and the directions of observed relationships between these variables were inconsistent (Table 5).

<i>Plant species</i>	<i>Bee species</i>	<i>Caste</i>	<i>p-value</i>	<i>R²</i>
<i>D. nuttallianum</i>	<i>B. appositus</i>	queen	0.058	0.075
<i>D. barbeyi</i>	<i>B. appositus</i>	worker	0.061	0.073
<i>A. columbianum</i>	<i>B. appositus</i>	worker	0.74	0.0024
<i>A. columbianum</i>	<i>B. flavifrons</i>	worker	0.86	0.00070

Table 5: Relationship between time spent on a flower and a bee's decision to remain on an inflorescence.

The nectar volume available for each species of plant differed very significantly ($p < 0.0001$; Table 6). Furthermore, the theoretical net rates of energy intake for *D. barbeyi* and *A. columbianum*, which grow together in patches and bloom simultaneously, also differed significantly, where *D. barbeyi* resulted in a much higher net rate of energy intake than *A. columbianum* (ANOVA, $p < 0.0001$; Figure 2).

<i>Species</i>	<i>Mean nectar volume (uL)</i>	<i>Standard error mean</i>
<i>D. nuttallianum</i>	0.18	0.023
<i>D. barbeyi</i>	0.32	0.021
<i>A. columbianum</i>	0.13	0.015

Table 6: Mean nectar volume per plant species.

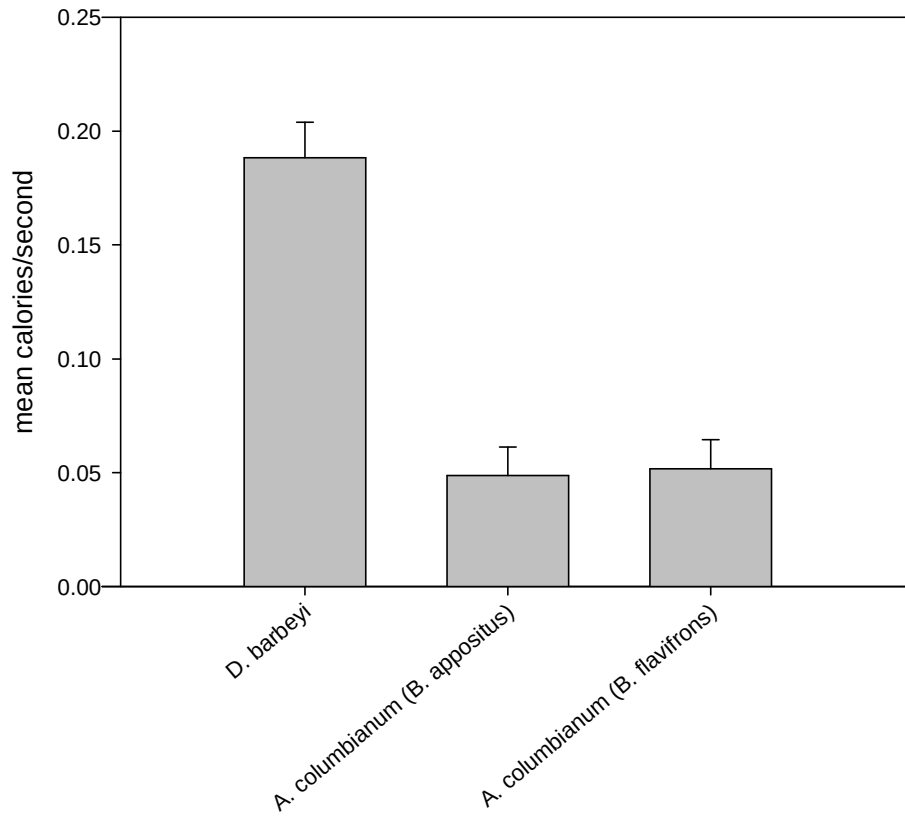


Figure 2: Mean rates of energy intake per species from theoretical values.

The observed mean number of flowers visited was consistently higher than the expected (Table 7; where 1.0 uL was considered the most likely threshold used). This difference was significant for 2 of the 3 cases, *D. nuttallianum* and *A. columbianum* ($p=0.039$ and 0.003 , respectively), meaning that the predicted behavior was not a good model for actual foraging behavior.

<i>Species</i>	<i>Observed</i>	<i>Standard error mean</i>	<i>1.0 uL threshold</i>	<i>Standard error mean</i>
<i>D. nuttallianum</i>	2.059	0.40	1.17	0.054
<i>D. barbeyi</i>	1.80	0.19	1.52	0.15
<i>A. columbianum</i>	2.73	0.37	1.16	0.10

Table 7: Mean number of flowers visited per inflorescence for observed and expected behavior.

DISCUSSION

The difference between the observed and expected foraging behavior could have resulted because the thresholds set were inaccurate. Increments of 0.5 uL may have been too large, meaning that a value close to the actual threshold was not considered and therefore not tested. It is also possible that bees do not maintain the same threshold for an entire inflorescence. Rather, they may initiate foraging with one threshold that changes with each flower as they ascend the inflorescence. Because nectar volumes typically decrease with flower position on an inflorescence, it is likely that a bee's threshold may decrease, similarly, with flower position. This would have an effect on the amount of energy gained per flight, so although a bee may employ an array of thresholds they would most likely have to fit within certain margins to make each flight energetically worthwhile. Further investigations are required, however, to test this theory.

The fact that there was no relationship between the time spent on a flower and a bee's decision to remain on that inflorescence or depart for a new one may have resulted because of the differences that exist among individual bumblebee sizes and flower corolla lengths. For example, a smaller bee encountering a somewhat larger than normal flower may take more time extracting nectar than it otherwise would have. Because each flower and bee is slightly different and many were observed during the course of this study, the variation among sizes could possibly have affected the outcome. To attain more accurate results a repeat of this study would need to target individual bees and flowers to control variation at that level.

It was not surprising that *Bombus appositus* workers foraging on *D. barbeyi* and *A. columbianum* were found to differ significantly in mass. Although it was not possible to measure proboscis lengths in this study, it is assumed that bees having greater masses would also have longer proboscises. These findings are consistent with what was expected because flowers of *D. barbeyi* have longer corollas than do flowers of *A. columbianum*, so it follows that larger bees would be successful foraging on *D. barbeyi*.

As a possible result of this, bumblebees were found foraging on *A. columbianum* in spite of the fact that *D. barbeyi*, which blooms at the same time and often grows in patches with *A. columbianum*, offered considerably more nectar. *Delphinium barbeyi*'s

larger size may have been unmanageable to smaller bees, which out of necessity foraged on flowers offering an inferior nectar reward.

A host of prior studies by Pyke *et al.* found that bumblebees exhibit behavior that is consistent with optimal foraging theory, however, the results of this most recent work clearly indicate that this may not be the case. The use of new technology such as digital video probably helped make observations more accurate since they could be revisited as many times as was necessary. This could certainly have affected the outcome of this research effort in comparison to earlier ones. Previous work in this area should not be disregarded as a result of this study, however, it must be understood that bumblebee foraging behavior may not be best explained by optimal foraging theory. Although bumblebees have appeared to employ certain behaviors that can be described as optimal, it is likely that their behavior is too complex to be described using a single theory.

This work should be revisited in the future using larger sample sizes and a wider array of bumblebee species to enhance the accuracy of the results. Furthermore, those involved in future studies of this type should do so with the awareness that animal behavior is influenced by a wide variety of factors, so limiting descriptions of it to the constraints of a concept such as optimal foraging theory may very well be an error.

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