Bumblebee Foraging at a "Hummingbird" Flower: Reward Economics and Floral Choice

John M. Pleasants; Nickolas M. Waser

American Midland Naturalist, Vol. 114, No. 2 (Oct., 1985), 283-291.

Stable URL:
http://links.jstor.org/sici?sici=0003-0031%28198510%29114%3A2%3C283%3ABFAA%22F%3E2.0.CO%3B2-L

American Midland Naturalist is currently published by The University of Notre Dame.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at http://www.jstor.org/about/terms.html. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at http://www.jstor.org/journals/notredame.html.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

http://www.jstor.org/
Sat May 7 10:31:56 2005

Bumblebee Foraging at a "Hummingbird" Flower: Reward Economics and Floral Choice

JOHN M. PLEASANTS[1], and NICKOLAS M. WASER[2]
Rocky Mountain Biological Laboratory, Crested Butte, Colorado 81224

ABSTRACT: For a brief period in 1981 *Bombus appositus* queens visited *Ipomopsis aggregata,* a hummingbird-pollinated species with floral characteristics typical of that pollination syndrome. This behavior was not observed in other years. Despite the fact that *Ipomopsis* lacks floral features associated with bee visitation, bumblebees foraged on *Ipomopsis* at a rate only somewhat slower than that for a typical bee flower. Because of the deep corolla, bumblebees are able to probe only a limited distance into *Ipomopsis* flowers but in 1981 nectar was more accessible due to a higher standing crop than in other years. While foraging on *Ipomopsis,* bees were able to obtain a net energetic profit which was similar to that obtained from their primary forage species. These observations indicate that floral choice is governed primarily by profitability—which can overcome innate preferences for bee flowers—and that the features of hummingbird flowers pose no absolute barrier to bee visitation. Bees apparently sample a wide spectrum of available flower types and will cross pollination syndrome lines if the reward economics are favorable.

INTRODUCTION

What factors determine how pollinators choose flowers? Two alternative answers can be distinguished (Waser, 1983). The first is related to the idea of "pollination syndromes" (*e.g.,* van der Pijl, 1961, Baker and Hurd, 1968; Faegri and van der Pijl, 1979; Kevan and Baker, 1983), which in extreme form proposes that pollinators differ in their innate preferences for floral attributes such as color, shape and scent. These attributes are said to occur in specific combinations—syndromes—that correspond to preferences of major pollinator types (red, tubular, scentless flowers for birds; blue asymmetrical, sweetly scented flowers for bumblebees, etc.). A corollary of this idea is that the exclusive relationship between a pollinator type and a syndrome is reinforced by the fact that the pollinator is excluded, physically or behaviorally, from flowers belonging to other syndromes. An alternative view holds that pollinator preferences for specific character syndromes are weak at best, and that it is largely the quantity and quality of food rewards that dictate floral choice (Pleasants, 1981, 1983a; Waser, 1983).

In 1981 we observed a large number of *Bombus appositus* queens foraging on *Ipomopsis aggregata,* a typical hummingbird flower. This was the only time this phenomenon occurred in a decade of observation of *Ipomopsis* (1975-1984). This event allowed us to examine the degree to which the attributes of hummingbird flowers that do not correspond to the bee syndrome might inhibit or exclude bumblebee visitation. These attributes include the following: The flower is scentless. Bumblebees use odor cues for attraction and orientation (Norris, 1983). The corolla lip lacks a landing platform for bees. The corolla is red. Bees are insensitive to most wavelengths in the red. The nectar sugar concentration is much lower than that in typical bee flowers [26% for *Ipomopsis* vs. 41.6% average for bee flowers (Pyke and Waser, 1981)]. Most importantly, the corolla depth of *Ipomopsis* exceeds the proboscis length of bumblebees. Bumblebees can only obtain nectar from flowers which have sufficient accumulated nectar in the corolla tube. As a result of previous work on *Ipomopsis* we had information on the standing crop of nectar, and thus the accessibility of the nectar to bumblebees, in other years. We therefore had an opportunity to measure the economics of bumblebee foraging on *Ip-*

[1]Department of Botany, Iowa State University, Ames 50011
[2]Department of Biology, University of California, Riverside 92521

omopsis and to examine whether bumblebee choice of *Ipomopsis* as a forage species in 1981 was determined by profitability.

There have been other reports of bumblebees visiting hummingbird flowers (Bertin, 1982; Harder, 1983). However, the present paper is the first attempt to ascertain the conditions which favor this floral choice.

MATERIALS AND METHODS

Ipomopsis aggregata (scarlet gilia; Polemoniaceae) is a common perennial monocarpic herb in mountains of western North America. At the Rocky Mountain Biological Laboratory (RMBL, elevation 2900 m) in Colorado its red tubular flowers are visited primarily by broad-tailed and rufous hummingbirds (*Selasphorus platycercus* and *S. rufus*), and more rarely by nectar-seeking hawkmoths (*Hyles lineta*) and swallowtail butterflies (*Papilio rutulus*), nectar-robbing bumblebees (*Bombus occidentalis*) and pollen-collecting Halictid bees (Waser, 1978, 1982).

To evaluate the efficiency of bumblebees foraging on *Ipomopsis* we followed bees and recorded their foraging speed (flowers/s). We also measured the travel and handling-time components of foraging speed. We compared the values of these parameters to those for *Bombus appositus* queens foraging on *Delphinium nelsonii,* a typical bee flower (blue-purple flower color; asymmetrical shape with a landing platform; sugar concentration - 51%; corolla depth - 18.6 mm), and the primary forage species for *B. appositus* queens. Foraging data for bees on *Delphinium* come from Hodges (1981) and Hodges and Wolf (1981). We could not directly compare handling times for *Ipomopsis* and *Delphinium* because bees obtained different average amounts of nectar from them. Handling time is the sum of access time (time for a bee to position itself at the flower and insert and retract its proboscis) and nectar extraction time (which is positively related to the amount of nectar received (Hodges and Wolf, 1981; Harder, 1983). Consequently, we used a handling time for *Delphinium* for the same amount of nectar as bees obtained from *Ipomopsis* (1.3 μl—*see below*). This handling time was calculated from the function $Y = 0.777 + .746X - 0.061X^2$ where X is the nectar obtained and Y is the handling time (Hodges and Wolf, 1981). We also compared the net rate of energy intake (NREI) for *B. appositus* queens on *Ipomopsis* and *Delphinium* using a standard formula (Appendix 1).

During 1981 and in other years we measured nectar standing crops in flowers by removing corollas and squeezing the nectar into microcapillary tubes. In 1981, to determine accessibility of nectar, we also measured corolla lengths and distances from the corolla tube opening to the line formed by the top of the nectar column within the corolla tube. To determine how deeply bees could actually probe flowers we measured quantities of nectar left behind, and distances to the nectar column, in flowers they had just visited. It is necessary here to exclude flowers where bees were unable to reach the nectar. We used handling time as an indicator of whether a bee obtained a reward or not (Hodges and Wolf, 1981, Harder, 1983). A short time spent at a flower reflects the case in which the bee probed the flower but received no reward. Longer handling times represent situations where bees were able to reach nectar: and amounts left over, in this case, should indicate the nectar threshold. We captured several individuals for measurement of proboscis length (prementum plus glossa: Macior, 1974). We also estimated abundances of male hummingbirds and *Ipomopsis aggregata* flowers every few days. All work took place in a single 0.5-ha study meadow at the RMBL. Because bumblebee visitation of *Ipomopsis* was so short-lived it was not possible to obtain all the relevant data that we would have desired.

RESULTS

Bombus appositus queens began foraging for nectar on *Ipomopsis aggregata* 26 June 1981, and had stopped by 10 July. Except for this time period, in a decade of observation of *Ipomopsis* (1975-1984) only two individual *B. appositus* queens were ever observed

on *Ipomopsis*. According to the pollinator syndrome idea, bees do not visit hummingbird flowers because characteristics of these flowers make foraging inefficient. If this is the case, bees should have a much slower foraging speed on *Ipomopsis* than on a bee flower such as *Delphinium nelsonii*. (Table 1) Foraging speed is broken down into its handling and travel time components to determine where any foraging inefficiency might occur. Table 1 also compares the net rate of energy intake (NREI) for bumblebees on *Ipomopsis* and *Delphinium*. The NREI for *Ipomopsis* is based on bees obtaining an average nectar volume of 1.3 μl per flower (*see below*). The calculations for NREI are shown in Appendix 1.

How accessible to bumblebees was the nectar in *Ipomopsis* flowers? Corolla tube length was 26.1 ± 0.29 mm (n = 129). In a flower sample from 5 July, the distance from the corolla mouth to the nectar column was 21.7 ± 0.36 mm (n = 101) (Fig. 1), and the nectar volume was 3.9 ± 0.29 μl (n = 99). *Bombus appositus* queens are the longest-tongued bumblebee residents in the immediate RMBL area, with a proboscis length of 15.0 ± 0.33 mm (n = 8). They were able to reach farther into corolla tubes than proboscis lengths suggest, by pushing their heads into the corolla. Bees were unable to reach all of the nectar, however, as indicated by volumes left behind in flowers just visited (2.6 ± 0.22 μl n = 73 on 5 July). The average amount of nectar that bees obtain per flower is 1.3 μl, the difference between the average standing crop (3.9 μl) and the average amount left behind per visit (2.6 μl).

What is the threshold nectar standing crop necessary for bees to obtain a reward? This threshold will be indicated by the lowest level to which bees can reduce the nectar column. Handling times for flowers ranged from less than 0.5 sec to nearly 9 sec (Fig. 2). To be certain we were dealing with flowers where bees had been able to reach the nectar, we considered only those where bees had spent ≥ 1.5 sec. That these were in fact "rewarding" flowers is shown by the greater amount of leftover nectar and the higher nectar column they had compared to flowers where bees spend < 1.5 sec. Based on what is left over in rewarding flowers, we estimate the maximum probing distances for *Bombus appositus* queens to be 21.2 mm and the mean nectar volume threshold to be 3.5 μl (Table 2). Taking our estimate of the distance threshold, and using the distribution of distances to the nectar column (Fig. 1), we calculate that 48% of all flowers contained enough nectar to provide some reward.

How did accessibility of nectar in 1981 compare to other years when bumblebees did not forage on *Ipomopsis*? Measurements over several years (Table 3) indicate that mean nectar standing crops of flowers were unusually high in 1981: only the two values from 1977 were approximately as high.

TABLE 1.—Foraging parameters for *Bombus appositus* on *Ipomopsis aggregata* and on *Delphinium nelsonii*, a bee-flower. *Delphinium* data are from Hodges (1981) and Hodges and Wolf (1981). For *Ipomopsis* foraging data mean ± 1 SE are given with sample size in parentheses

	Ipomopsis aggregata	*Delphinium nelsonii*
Foraging speed (flower/s)	.21 (1314)	.34
Handling time (s)	1.83 ± .10 (195)	1.65
Travel time (s)		
within inflorescences	1.88 ± .10 (115)	.71
between inflorescences	3.91 ± .34 (74)	1.69
Net rate of energy intake (NREI) (cal/s)	.21	.35

DISCUSSION

These results suggest that floral choice by the bumblebees is sensitive to reward economics, and that this overrides any innate prejudice that may exist against the floral characteristics of the "bird pollination syndrome."

The floral features of *Ipomopsis* do not strongly inhibit bumblebee foraging as seen when foraging parameters are compared with those for *Delphinium,* a typical bee flower (Table 1). Overall, the rate of visitation to *Ipomopsis* flowers was ⅔ that for *Delphinium.* This slower foraging speed could be due to inefficiency in handling the flowers or in searching for them (travel time). Handling time was similar for both species. Travel time between flowers within the inflorescence was greater for *Ipomopsis* but this may be due to wider spacing of flowers on the *Ipomopsis* inflorescence. For example, travel time between flowers of *Aconitum columbianum,* a bee flower with wider flower spacing than *Delphinium,* is 1.55 sec (Pyke, 1978), a value similar to that for *Ipomopsis.* Travel time between plants was over twice as long for *Ipomopsis.* This can be explained in part by the greater interplant distance for *Ipomopsis* (.83 m vs .15 m for *Delphinium*). But *Aconitum* interplant distance (1 m) is even greater than for *Ipomopsis,* yet travel time for queens is only 1.65 sec (Pyke, 1978). Thus the slower travel time may represent some inefficiency associated with searching for flowers lacking strong visual and odor cues. Bees were occasionally observed to collide with leaves and stems when going from one flower to another.

It is often stated that bees cannot see red and/or are not attracted to red flowers (Grant and Grant, 1968; Raven, 1972; Faegri and van der Pijl, 1979; Waddington, 1983). However, honeybees and bumblebees have spectral sensitivity that extends slightly into the red (650 nm) (Autrum, 1968; Menzel *et al.,* 1974; Kugler, 1943;

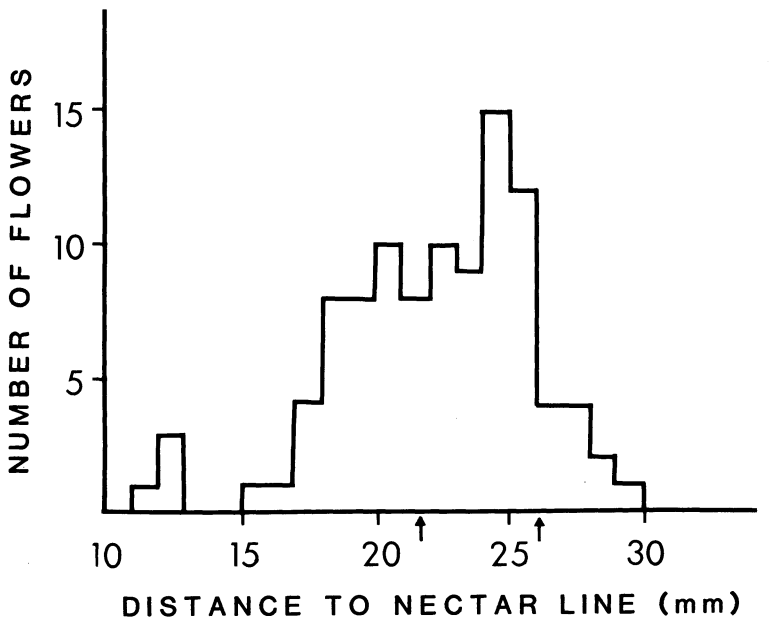

Fig. 1.—The frequency distribution of distances from corolla mouths to tops of nectar columns, from a sample of *I. aggregata* flowers taken on 5 July 1981. The left arrow indicates the estimated maximum probing distance for *B. appositus* queens; the right arrow indicates the average corolla length

Mazokhin-Porshnyakov, 1969). Also, hummingbird flowers such as *Ipomopsis* that are described as "red" without exact colorimetric analysis are often likely to reflect in red-orange wavelengths below 650 nm. Even if flower color is outside the range of spectral sensitivity, the flower would not be invisible but would simply appear as "black." What our behavioral observations of *Bombus appositus* at *I. aggregata* flowers confirm, certainly, is that the bees associate the visual cues of these flowers with a food reward (as do *B. occidentalis* and Halicitids that also visit flowers every year in small numbers), so that color presents no absolute barrier to visitation.

A similar point can be made with regard to *Ipomopsis aggregata* nectar concentration, which is characteristic of "hummingbird" flowers in being relatively dilute (Pyke and Waser, 1981; Appendix 1). Although Bolten and Feinsinger (1981) have proposed that bees will not be able to make an energetic profit with dilute nectars and will avoid them, we are aware of no strong support for these ideas. Bees often use dilute nectars (*see, e.g.,* Free, 1970, Chap. 2; Pleasants, 1981, Table 1; Pyke and Waser, 1981, Table 3; Roubik and Buchmann, 1984), even though they prefer concentrated ones when given a choice (Waller, 1972; Roubik and Buchmann, 1984).

The only feature that could pose an absolute barrier to visitation is corolla depth. In 1981, because of the large standing crop, nectar was accessible in 48% of the flowers, although even for these flowers bees could only skim the nectar that was above a certain threshold. With a lower standing crop, a smaller proportion of flowers will have accessible nectar and profit will be reduced. We cannot specify an average standing crop level

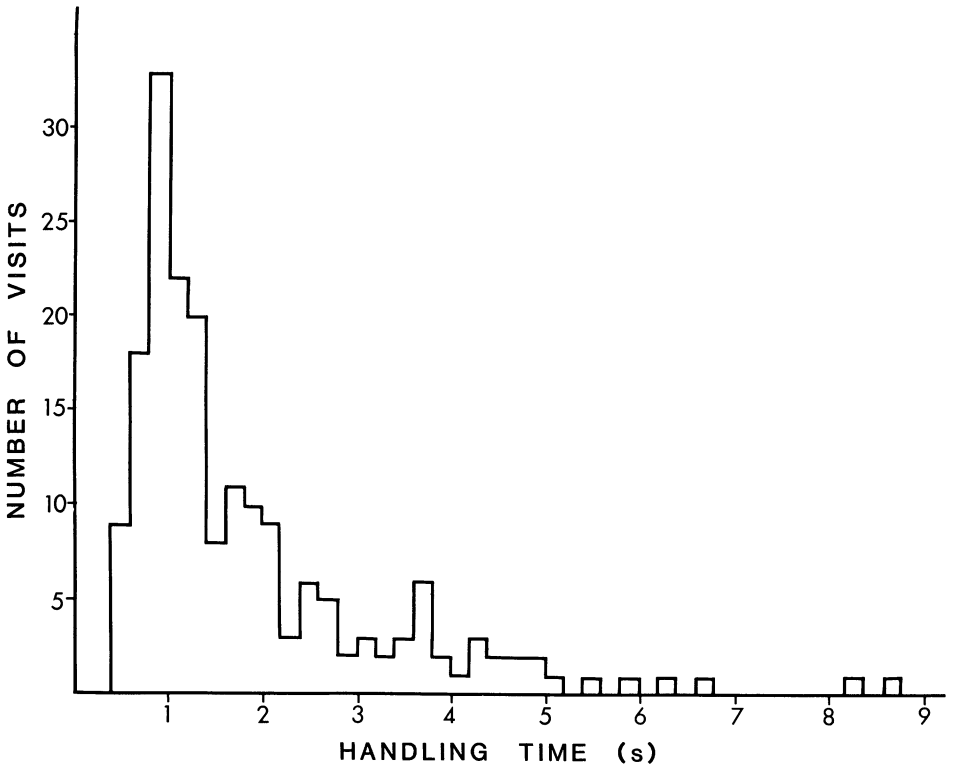

Fig. 2.—The distribution of handling times of *B. appositus* queens on *I. aggregata* flowers, from 3 July 1981

below which *Ipomopsis* would be absolutely unacceptable to *Bombus appositus* queens. Certainly, foraging queens require a NREI greater than the break-even point, but we do not know what the lowest acceptable profit margin is and it may vary depending on economic necessity. Perhaps *Ipomopsis* in 1981 had just entered the realm of acceptability. This would explain why we observed only two visits to *Ipomopsis* in other years, even though in some years standing crops were not substantially lower than in 1981.

The NREI for bees on *Ipomopsis* is only ⅔ of the NREI for bees on *Delphinium* (Table 1). However, this should not be used to conclude that *Ipomopsis* was a poor choice. First we have used as a reference standard the NREI for bumblebee queens foraging on *Delphinium*. This NREI was based on standing crops averaged over several sample periods in July 1979 (Hodges, 1981). But standing crops lower than this have been observed (Pleasants and Zimmerman, 1979), so queens may often be foraging with a NREI as low as for *Ipomopsis*. Second, *Delphinium* completes flowering about the time *Ipomopsis* begins to bloom (Waser, 1978), so during the period in 1981 when bees were visiting *Ipomopsis, Delphinium* was not an available choice. Two other species were available at this time, *Vicia americana* and *Lathyrus leucanthus,* both of which are primarily visited by *Bombus appositus* (Pleasants, 1977). However, due to the ephemeral nature of the *Ipomopsis* visitation phenomenon we were not able to obtain NREI value for these species. Thus, although we can say that visiting *Ipomopsis* was profitable, we cannot evaluate whether it represented an optimal flower choice.

What was different about 1981 that led to high nectar standing crops? *Ipomopsis* began blooming in 1981 much earlier than in other years. Initiation dates for flowering for 1975-1982 are as follows: 1975-8 July; 1976-26 June; 1977-18 June; 1978-28 June; 1979-1 July; 1980-3 July; 1981-13 June; 1982-4 July. Hummingbird numbers increase markedly during July because of the influx of *Selasphorus rufus* during its southward mi-

TABLE 2. — Nectar characteristics and handling times of flowers visited by *B. appositus* during 1981. Values are means ± 1 SE, sample size in parentheses. Data from 7, 8 July 1981

Flower sample[a]	Leftover nectar[b] (μl)	Distance to nectar column[c] (mm)	Handling times[d] (s)
Rewarding	3.5 ± 0.39 (22)	21.2 ± 0.56 (22)	2.8 ± 0.30 (22)
Unrewarding	2.1 ± 0.37 (26)	22.8 ± 0.53 (26)	0.9 ± 0.06 (26)

[a] "Rewarding" flowers are those with handling times ≥ 1.5sec, while "Unrewarding" flowers are those with handling times < 1.5 sec

[b] Standing crops taken immediately after flowers were visited; means for "rewarding" and "unrewarding" flowers differ at P = 0.004 (Mann-Whitney U = 392.5)

[c] Distance from the corolla mouth to the nectar following visitation. Means for "rewarding" and "unrewarding" flowers differ at P = 0.04 (Mann-Whitney U = 173)

[d] Time spent by bees probing each flower

TABLE 3. — Nectar standing crops of *I. aggregata* flowers in the study meadow. Values are in μl and are means ± 1 SE with sample size in parentheses

Date	Standing Crop	Date	Standing Crop
8 July 1975	2.5 ± 0.41 (17)	5 July 1981 (1030-1200 hrs)	3.9 ± 0.29 (99)*
18 July 1975	1.2 ± 0.25 (48)	5 July 1981 (1530-1645 hrs)	3.0 ± 0.22 (98)*
20 June 1976	0.1 ± 0.03 (10)	6 July 1981	3.7 ± 0.40 (23)*
11 July 1976	1.2 ± 0.29 (25)	10 July 1981	3.2 ± 0.41 (20)
14 July 1976	0.9 ± 0.18 (26)	12 July 1982	2.5 ± 0.15 (150)
8 July 1977	3.1 ± 0.36 (42)	15 July 1984	1.4 ± 0.30 (32)
9 July 1977	3.7 ± 0.33 (39)	21 July 1984	1.0 ± 0.17 (29)
19 July 1978	0.1 ± 0.05 (35)		

*These values fall within the period of intensive *B. appositus* foraging

gration through RMBL. This usually coincides with the peak of *Ipomopsis* flowering. In 1981, however, plants were in full bloom before the hummingbird population buildup. This is indicated by the change in hummingbird-to-flower ratio from periodic censuses (Table 4). The single value of the bird-to-flower ratio from the period of intensive *Bombus appositus* foraging was smaller than any other 1981 value. This asynchrony led to a period of undervisitation by hummingbirds and thus a higher standing crop. Based on a 24-hr nectar production of 4 μl for *Ipomopsis* (Pleasants, 1983b), the 5 July standing crop of 3.9 μl indicates that flowers were receiving on average one visit per day. Interestingly, *Ipomopsis* also bloomed early in 1977 and this was the only other year which had nectar standing crops as high as in 1981 (*see* Table 3). Why did bumblebees not visit *Ipomopsis* in 1977? One possible explanation is provided by the fact that 1977 (but not 1981) was a year of great abundance for *Frasera speciosa,* the monument plant (Taylor and Inouye, 1985). This monocarpic species is characterized by sporadic mass flowering. It produces abundant nectar and is highly attractive to bumblebees (Beattie *et al.,* 1973). The presence of this "cornucopia" during 1977 may have rendered *Ipomopsis* relatively unprofitable by comparison.

Why was the bumblebee visitation phenomenon so short-lived (14 days)? The end (10 July) did not coincide with a sudden drop in standing crop (*see* Table 3). However, it did coincide with an increase in hummingbird activity (Table 4). Hummingbirds sometimes attack bumblebees such as the nectar-robbing *Bombus occidentalis* on *Ipomopsis* (pers. observ.), so bumblebees might have been driven away. Reduced visitation may also have resulted from a general disappearance of *Bombus appositus* queens as foragers. Queens forage for a limited time early in the season, then return permanently to their nests to raise workers. By the middle of July queens are seldom seen (Pleasants, 1977). *Bombus appositus* workers have a shorter proboscis than queens and were never observed on *Ipomopsis.*

These observations indicate that bumblebees explore flowering species beyond those within their own coadapted domain. Whether they do this routinely or are more apt to do it when species within their domain become less profitable is not known. For a species to be included in a bee's diet it must have a reward value that is at least comparable to that of other forage species (Pleasants, 1981). Thus, *Ipomopsis* may have been included in 1981 because the higher standing crop in that year suddenly elevated it to a level of profitability competitive with available bee flowers. On the other hand, bees might have visited *Ipomopsis* not because the profits there were higher than usual but because the profits of available bee flowers were lower than usual, making *Ipomopsis* an acceptable alternative. This could have happened, for example, if bumblebee queen abundance was unusually high, leading to greater foraging activity and lower profits on bee

TABLE 4. — Results of censuses of hummingbirds and *I. aggregata* flowers during 1981

Date	Flower Density[a]	Hummingbird Activity[b]	Bird-to-Flower Ratio[c]
16 June	1.3	14	10.8
20 June	3.6	11	3.1
6 July	17.5	23	1.3[d]
10 July	16.5	50	3.0
14 July	13.8	42	3.0
21 July	7.6	20	2.6
29 July	5.4	11	2.0

[a] Mean number of flowers per 2 m by 2 m permanent census plot in the study meadow
[b] Number of audible flights of *S. platycercus* and *S. rufus* during a standard 10-minute census period in the study meadow
[c] This ratio has arbitrary but constant dimensions of flights per 10 min/flowers per 4 m^2
[d] This value falls within the period of intensive *B. appositus* foraging

flowers, or if the abundance of available bee flowers was unusually low. Because we lack baseline data on bumblebee and flower abundance in other years it is not possible to evaluate the importance of these factors. In any case, we can say that bees have the flexibility to capitalize on any profitable opportunity that arises. It should be noted that bumblebee visitation has potential significance for *Ipomopsis* as well. It may represent a fall-back pollination option in times of hummingbird scarcity. Of eight individual bumblebees we examined, all carried substantial pollen loads on their heads and mouthparts.

APPENDIX 1. CALCULATION OF NET RATE OF ENERGY INTAKE (NREI)

$$\text{NREI} = \frac{\text{VCS} - T_h\,(M_h) - T_t\,(M_t)}{T_h + T_t}$$

where

V = average volume of nectar obtained from flowers (1.3 μl);
C = sugar concentration of the nectar (26.0% sucrose-equivalent sugars weight by volume (from 5 July data));
S = caloric content of sucrose (3.7 cal/mg);
T_h = average handling time per flower (1.9 s);
T_t = average travel time between flowers (3.02 s; includes travel between inflorescences);
M_h = metabolic cost of flower handling for a *B. appositus* queen (0.00483 cal/s; Pyke, 1980);
M_t = metabolic cost of flight (0.0625 cal/s; Pyke, 1980).

Based on these values, the NREI is 0.21 cal/s.

Acknowledgments.—We thank Mary Price, Bob Neely, Mark Pelham and Paul Rich for field assistance; Peter Feinsinger, Mary Price, Barbara Yohai Pleasants and Arthur Yohai for insightful comments on the manuscript; and NSF grants DEB 8102774 and BSR 8313522 (to NMW) and DEB 8111027 (to JMP) for financial support.

LITERATURE CITED

AUTRUM, H. 1968. Colour vision in man and animals. *Naturwissenschaften,* **55**:10-18.
BAKER, H. B. AND P. D. HURD. 1968. Intrafloral ecology. *Annu. Rev. Entomol.,* **13**:385-414.
BEATTIE, A. J., D. E. BREEDLOVE AND P. R. EHRLICH. 1973. The ecology of the pollinators and predators of *Frasera speciosa. Ecology,* **54**:81-91.
BERTIN, R. I. 1982. Floral biology, hummingbird pollination and fruit production of trumpet creeper (*Campsis radicans,* Bignoniaceae). *Am. J. Bot.,* **69**:122-134.
BOLTEN, A. B. AND P. FEINSINGER. 1981. Why do hummingbird flowers secrete dilute nectar? *Biotropica,* **10**:307-309.
FAEGRI, K. AND L. VAN DER PIJL. 1979. The principles of pollination ecology, 3rd ed. Pergamon Press, Oxford. 244 p.
FREE, J. B. 1970. Insect pollination of crops. Academic Press, London. 544 p.
GRANT, K. A. AND V. GRANT. 1968. Hummingbirds and their flowers. Columbia Univ. Press, New York. 115 p.
HARDER, L. D. 1983. Flower handling efficiency of bumblebees: morphological aspects of probing time. *Oecologia,* **57**:274-280.
HODGES, C. L. 1981. Optimal foraging in bumblebees: hunting by expectation. *Anim. Behav.,* **29**:1166-1171.
HODGES, C. M. AND L. L. WOLF. 1981. Optimal foraging in bumblebees: why is nectar left behind in flowers? *Behav. Ecol. Sociobiol.,* **9**:41-44.
KEVAN, P. G. AND H. G. BAKER. 1983. Insects as flower visitors and pollinators. *Annu. Rev. Entomol.,* **28**:407-453.
KUGLER, H. 1943. Hummeln als Blutenbesucher. *Ergeb. Biol.,* **19**:143-323.

MACIOR, L. W. 1974. Pollination ecology of the front range of the Colorado Rocky Mountains. *Melanderia,* **15**:1-59.

MAZOKHIN-PORSHNYAKOV, G. A. 1969. Insect vision. Plenum Press, New York. 306 p.

MENZEL, R., J. ERBER AND T. MASUHR. 1974. Learning and memory in the honeybee, p. 195-217. *In*: L. B. Browne (ed.). Experimental analysis of insect behavior. Springer, New York.

NORRIS, W. H. 1983. Floral fragrances as cues in animal behavior, p. 50-72. *In*: C. E. Jones and R. J. Little (eds.). Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, N. Y.

PLEASANTS, J. M. 1977. Competition in plant-pollinator system: An analysis of meadow communities in the Colorado Rocky Mountains. Ph.D. dissertation, University of California, Los Angeles. 233 p.

_____. 1981. Bumblebee responses to variation in nectar availability. *Ecology,* **62**:1648-1661.

_____. 1983a. Structure of plant and pollinator communities, p. 375-393. *In* C. E. Jones and R. J. Little (eds.). Handbook of experimental pollination biology. Van Nostrand Reinhold, New York.

_____. 1983b. Nectar production patterns in *Ipomopsis aggregata* (Polemoniaceae). *Am. J. Bot.,* **70**:1468-1475.

_____ AND M. ZIMMERMAN. 1979. Patchiness in the dispersion of nectar resources: Evidence for hot and cold spots. *Oecologia,* **41**:283-288.

PYKE, G. H. 1978. Optimal body size in bumblebees. *Ibid.,* **34**:255-266.

_____. 1980. Optimal foraging in bumblebees: calculation of net rate of energy intake and optimal patch choice. *Theor. Pop. Biol.,* **17**:232-246.

_____ AND N. M. WASER. 1981. The production of dilute nectars by hummingbird and honeyeater flowers. *Biotropica,* **13**:260-270.

RAVEN, P. H. 1972. Why are bird-visited flowers predominately red? *Evolution,* **26**:674.

ROUBIK, D. W. AND S. L. BUCHMANN. 1984. Nectar selection by *Melipona* and *Apis mellifera* (Hymenoptera:Apidae) and the ecology of nectar intake by bee colonies in a tropical forest. *Oecologia,* **61**:1-10.

TAYLOR, D. R., JR. AND D. W. INOUYE. 1985. Synchrony and periodicity of flowering in *Frasera speciosa* (Gentianaceae). *Ecology,* **66**:521-527.

VAN DER PIJL, L. 1961. Ecological aspects of flower evolution. II Zoophilous flower classes. *Evolution,* **15**:44-59.

WADDINGTON, K. D. 1983. Foraging behavior of pollinators, p. 213-239. *In*: L. A. Real (ed.). Pollination biology. Academic Press, New York.

WALLER, G. D. 1972. Evaluating responses of honey bees to sugar solutions using an artificial-flower feeder. *Ann. Entomol. Soc. Am.,* **65**:857-862.

WASER, N. M. 1978. Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology,* **59**:934-944.

_____. 1982. A comparison of distances flown by different visitors to flowers of the same species. *Oecologia,* **55**:251-257.

_____. 1983. The adaptive nature of floral traits: Ideas and evidence, p. 241-285. *In*: L. A. Real (ed.). Pollination biology. Academic Press, New York.

SUBMITTED 25 JUNE 1984 ACCEPTED 21 FEBRUARY 1985