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The Effect of Proboscis and Corolla Tube Lengths on Patterns and Rates of Flower Visitation by Bumblebees

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Summary. The rates at which bumblebees of different proboscis lengths forage on flowers of a series of corolla tube lengths were determined. The results indicate significant correlations between proboscis length and time spent by bees on flowers. Bumblebees of long proboscis length can forage significantly faster than bees of shorter proboscis length on flowers with long corolla tubes. There is also evidence which suggests that bumblebees of short proboscis length prefer and are more efficient on short corolla tubes. These results support the use of proboscis length as a morphological indicator of resource utilization in bumblebees.

Introduction

The number and relative abundance of species in natural communities are phenomena which have occupied the attention of many ecologists. Studies of resource partitioning provide one method of investigating the limits which interspecific competition places on the number of species that can stably coexist (Schoener, 1974), and biologists have often estimated resource differences by using morphological characteristics that are assumed to reflect differences in resource utilization (Hespenheide, 1973). The commonest such indicators are dimensions of feeding structures, which are usually correlated with mean food size, hardness, or depth in some protective medium. This study was undertaken to determine the actual significance of proboscis length of bumblebees as a morphological indicator of resource utilization. Although previous studies have concluded that proboscis length is related to differences in flower visitation (e.g., Hobbs, 1962; Hobbs, et al., 1961; Cumber, 1949), this study was designed to quantify the relationship for bees in a natural flower community.

Methods

Although some references fail to define their measurements accurately, "proboscis length" of bumblebees is generally accepted to refer to the length of the labium, or the combination of the prementum and the glossa. The bumblebee proboscis can be assumed to operate in the same manner as that of the honeybee (Knutz, 1906). The maxillary galeae and the labial palpi are brought to-

gether around the glossa to form a proboscis for the intake of liquids (Snodgrass, 1956). The glossa is essentially a muscular tube covered with short hairs. When it comes into contact with the nectar at the bottom of a corolla tube, capillary action draws nectar up to its base (Knutz, 1906). The pre-oral food-receiving pocket, or cibarium, functions as a sucking pump to draw liquids up through the tube. When not in use, the maxillae and labium are separated and folded back below and behind the head (Snodgrass, 1956).

The data on proboscis lengths of queens and workers presented in Fig. 2 were taken from published measurements of bumblebees collected on the Front Range of the Colorado Rocky Mountains (i.e., east of the Continental Divide) (Macior, 1974). Measurements indicate the sum of the individual lengths of the prementum and glossa. In reality the proboscis length is 5–10% longer, due to the presence of connective tissue. Small samples of workers and queens indicated that there was no significant difference in proboscis length between the Front Range and western Colorado populations of a species. To determine the actual depth from which nectar can be extracted by a bumblebee ("total effective foraging length", Macior, 1978), the length of the head and even part of the thorax must be added to the proboscis length if the mouth of the corolla being visited is wide enough to accommodate them. However, these measured proboscis lengths are still useful for comparing nectar-foraging rates (Macior, 1978).

Data on flower sizes and bee visitation rates were collected in the neighborhood of the Rocky Mt. Biological Laboratory, Gothic, Colorado. Corolla tube lengths of freshly picked flowers from different flower stalks and areas were measured to the nearest 0.001 inch with a vernier caliper. The measurements were chosen to reflect the actual distance that the bee must reach in order to extract nectar from the bottom of the corolla tube. Accumulation of nectar in the flower would reduce this distance. While distinct constrictions or fringes sometimes provide relatively reliable clues, it is not always obvious how far a bumblebee can insert its head and thorax into a flower. Some of the variance around the regression lines involving measurements of corolla tube length can be attributed to this measurement error.

The amount of time bumblebees spent visiting individual flowers was measured with a stopwatch. For composites (Asteraceae) the total amount of time a bee spent probing individual florets on a head was recorded and divided by the number of florets probed, to give a value of time per flower. Although this technique thus includes time spent moving between florets, which is not included in measurements for other flowers, the florets are in such close proximity that this component should be neglig-

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ible. The distribution of times per flower is always skewed to the right of a normal distribution, owing to a low but persistent level of unusually long times. These values occurred, for example, when a bee stopped to clean its proboscis while on the flower. On other occasions there was no obvious reason for the delay on a flower. These delays were not recorded or were subsequently discarded.

This value of "time per flower" is probably a combined measurement of handling time and extraction time. The former is the amount of time it takes to land on a flower, extend the proboscis, insert it into the flower as far as possible (or as far as necessary) by pushing the head into the flower, and then to withdraw the proboscis and leave the flower. Extraction time is the amount of time spent actually pumping or sucking the nectar out of the flower once the bee is in position. It seems reasonable to assume that extraction time would not be dependent on proboscis length, but that handling time would be. My observations suggest that extraction time is usually a negligible component of "time per flower", so I will assume "time per flower" is in effect a measure of handling time.

The amounts of nectar available in the flowers considered in this study are on the order of 0.1 to approximately 4.0 microliters. The amount of nectar in an individual composite floret is so small that it is usually impossible to extract it with a microliter syringe. It seems likely that most of this nectar would be picked up by capillary action almost immediately on contact with the proboscis. The bee would then suck up the nectar while removing its proboscis from the flower and flying to another. Such a possibility has been suggested for the hummingbird proboscis, which can hold about 0.8 microliters of nectar (Hainsworth, 1973). Goetze (1936, cited in Hawkins, 1969) found that if a honeybee can just touch the surface of the nectar in red clover flower, most of it can be extracted by capillary action.

Possible effects of variation in size within a caste of a single species were also investigated. Workers of *Bombus flavifrons* were collected as they foraged in an area in the East River Valley containing dense stands of *Mertensia ciliata* (mean corolla tube length 9.89 mm) and *Delphinium barbeyi* (mean corolla tube length 13.96 mm). The flower species occurred in more or less discrete clumps, and individual bees restricted themselves in most cases to one flower species. Body length, proboscis length, and radial cell length (a well defined area of the wing) were measured on all specimens with an optical micrometer in a binocular microscope. The radial cell measurement is probably most suitable for comparative investigation because it is heavily chitinized and significantly correlated with proboscis length (Pisani et al., 1968; Medler, 1962a, b; Morse, 1977).

Results

The relationship between proboscis length and the amount of time spent by bumblebee workers on flowers was examined in two ways. Figure 1 presents the data for workers of *B. flavifrons* foraging on eight of the flower species it visits most commonly, and data for seven different species or castes of bumblebees foraging on *Delphinium barbeyi* are shown in Fig. 2. The significant correlations shown for *B. flavifrons* in Fig. 1 and for four other species in Fig. 2 indicate that corolla tube length does affect time per flower. *B. flavifrons* workers visit flowers with short corolla tubes more rapidly than those with long corolla tubes, and a bee species with a long proboscis can visit *Delphinium* flowers faster than another species with a shorter proboscis. This conclu-

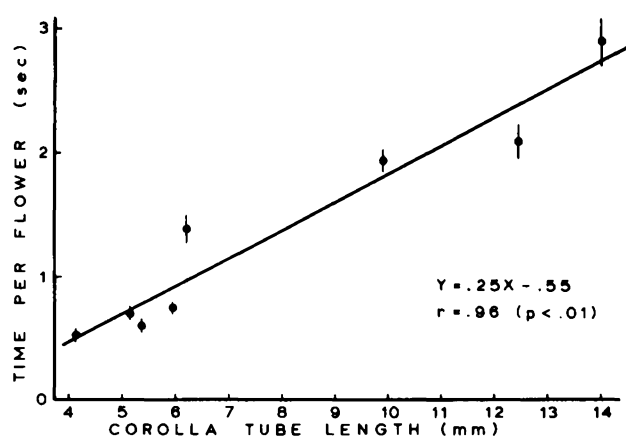


Fig. 1. Mean times per flower for *Bombus flavifrons* workers foraging on eight different species of flowers. Vertical lines indicate one standard error. Flower species, in order of increasing corolla tube length, are *Chrysopsis villosa* (4.11 mm), *Senecio bigelovii* (5.37 mm), *Helianthella quinquenervis* (5.9 mm), *Cirsium* sp. (6.17 mm), *Mertensia ciliata* (9.89 mm), *Vicia americana* (12.42 mm), and *Delphinium barbeyi* (13.96 mm)

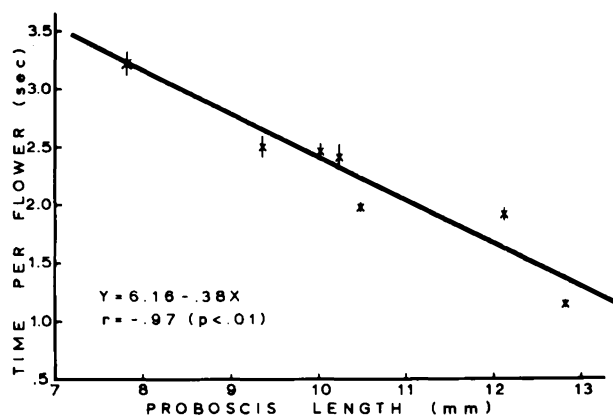


Fig. 2. Mean values of time per flower for bumblebees of different castes and species foraging on *Delphinium barbeyi*. Vertical lines indicate one standard error. Bees, in order of increasing proboscis length, are *B. flavifrons* workers, *B. kirbyellus* workers, *B. californicus* workers, *B. flavifrons* queens, *B. appositus* workers, *B. kirbyellus* queens and *B. appositus* queens

sion is supported by three additional examples involving three or four different bee species or castes visiting a single flower species (Table 1). In each of these there is a significant negative correlation between proboscis length and time per flower. Regression equations were calculated to describe these same relationships for queens of the three proboscis length classes. For all three classes, time per flower was positively correlated with corolla length, but the slope of the regression lines decreased with increasing proboscis length.

Regardless of corolla length, five other flower species visited by bees of only 2 proboscis lengths were visited more rapidly by the one with the longer proboscis. In one case, however, involving males of two species foraging on *Cirsium* sp., the species with the longer proboscis foraged slower than the other species, and for two flower species of short corolla length (3.07 and 5.94 mm) a pair of bee species of short proboscis length visited

Table 1. Regression equations of time per flower plotted against proboscis length, for 3 flower species. Y = mean time per flower, X = mean proboscis length. Bee species: 1 = *B. appositus* queens; 2 = *B. californicus* queens; 3 = *B. kirbyellus* queens; 4 = *B. flavifrons* queens; 5 = *B. sylvicola* queens; 6 = *B. appositus* workers; 7 = *B. flavifrons* workers

Flower species			<i>r</i>
<i>Mertensia ciliata</i>	3, 4, 5, 7	$Y = -0.17X + 3.16$	-0.956 ($p < 0.05$)
<i>Lathyrus leucanthus</i>	1, 2, 4, 5	$Y = -0.94X + 14.45$	-0.982 ($p < 0.05$)
<i>Vicia americana</i>	1, 6, 7	$Y = -0.11X + 2.94$	-0.999 ($p < 0.05$)

Table 2. Measurements of *Bombus flavifrons* workers collected while foraging on *Delphinium barbeyi* and/or *Mertensia ciliata*

		Body length	Radial cell	Pre-mentum	Glossa
<i>Delphinium barbeyi</i> N = 12	mean	14.37	2.84	2.91	6.25
	s.d.	1.23	0.37	0.18	0.28
<i>Mertensia ciliata</i> N = 11	mean	11.46	2.45	2.50	5.43
	s.d.	1.06	0.13	0.13	0.39
	<i>p</i> <	0.05	0.02	0.02	0.01
both N = 2	mean	13.47	2.73	2.97	6.45
	s.d.	0.72	0.06	0.03	0.22

All measurements are in mm

Differences in the means of bees on *Delphinium* and *Mertensia* are all significant ($p < 0.001$, τ -test)

Differences in the means of bees on *Delphinium* and both flowers are not significant (τ -test)

The levels of significance of differences between means of bees feeding on *Mertensia* and both flowers are indicated

flowers faster than the species with the next greater proboscis length.

There also appear to be significant differences in flower visitation within a caste of one species, which reinforce the conclusions from comparisons among species. Mean measurements of the *B. flavifrons* workers collected on *Delphinium* (the larger of the two flowers) were larger than those of bees collected on *Mertensia* (Table 2). The two individuals observed foraging on both species of flowers were intermediate in two of the four measurements taken, but are closer to the larger bees.

Discussion

In only a few cases has the nature of the relationship between resource utilization and morphological characteristics actually been investigated. Studies of the relationship between bill size characters of birds and the seeds they eat have given ambiguous results (Willson, 1971, 1972; Abbott et al., 1975), probably owing to the complication of studying a three-dimensional organ in which differences in depth, width, and height are important to varying degrees in different species (Hespenheide, 1966; Root, 1967). Proboscis length of bumblebees, however, appears to be a good morphological indicator of resource utilization in bumblebees (Figs. 1, 2; Table 1). In fact, bumblebees as well as other flower visitors appear to partition flower resources primarily on the basis of the relationship between proboscis length and the lengths of

the corolla tubes of the flowers available (Knuth, 1906; Schemske, 1976; Stiles, 1975; Teräs, 1976). In this relationship both the morphological indicator and the "protective medium" (corolla tube) can be considered to be one-dimensional: only length (depth) is important.

The literature on crop pollination provides additional evidence for a well-defined relationship between the proboscis length of bumblebees and honeybees and their speed of foraging. Benedek (1973) found a significant positive correlation between proboscis length and number of flowers visited per minute for 13 species of bees (including two species of bumblebees) foraging on lucerne. Stapel (1933) indicated the relative efficiencies of bees in pollinating clover by assigning a figure of 1.0 to queen bumblebees, 0.83 and 0.5 to long- and short-proboscis worker bees, respectively, and 0.33 to honeybees. Dennis and Haas (1967b), Holm (1966), Wojtowski (1965), and Stapel (1933) found that the working speed of bees in clover was closely correlated with proboscis length. Comparisons of diploid and tetraploid red clover also prove to be of interest. Although the mean corolla tube length of tetraploid clover is only 0.49 mm longer than that of diploid clover, there are differences between the two forms in visitation rates and the numbers and species of bees that visit them (Dennis and Haas, 1967a, b; Friden et al., 1962; Hawkins, 1969; Holm, 1966; Valle et al., 1960). These differences are consistent with those in proboscis length of the bee species involved. Similarly, Graenicher (1909) found significant differences in the proportions of pollinators of different proboscis lengths visiting nine species of *Aster*, whose corolla tube lengths ranged from 1 to 4 mm.

The evidence presented so far has generally supported the hypothesis that a bee species with a long proboscis visits flowers faster than a bee with a shorter proboscis. What, then, might be the advantage of a short proboscis? Kugler (1940) suggested that a long proboscis may be a hindrance in the collection of nectar from flowers of short corolla tube length, stating that a long-proboscis bee species "met with significantly more difficulty" than a short-proboscis species in feeding on honey droplets on a flat surface.

There are a number of flower species, for example most of the composites in my study areas, with corolla tube lengths of less than 6 mm (Inouye, 1979). Unfortunately it was almost impossible to collect data on queens foraging on these flowers for at least two reasons: 1) differences in the time of year when queens are foraging and when the composites are flowering; and 2) the apparent reluctance of bees of long proboscis length to feed on flowers of short corolla tube length. Data from two flower species, however, suggest that bees of short proboscis length can visit flowers with short corolla tubes faster than bees with long proboscides. Both *Frasera speciosa* (mean distance to nectar 3.0 mm) and *Helianthella quinquenervis* (mean corolla tube length 5.9 mm) are visited faster by bees of short and long proboscis length than

by bees of intermediate proboscis length (Inouye, 1976). The marked preference for composites shown by bumblebee species of short proboscis length, and the corresponding reluctance of bees of long proboscis length to visit the same flowers suggest the generality of the relationship. Poulsen (1973), studying the foraging behavior of honeybees and bumblebees on field beans in Denmark, found a similar result: *B. distinguendus* was able to visit more flowers per minute than bee species of longer and shorter proboscis length.

Skovgaard (1952, cited in Brian, 1954) suggested that differences in the speed with which flowers are visited are not entirely the result of differences in proboscis length. He found, for example, that workers of two species of similar proboscis length differed considerably in the number of flowers visited per minute. Similarly, handling times and patterns of flower visitation can also depend on aspects of floral morphology other than corolla length. An example is provided by two species of legumes in the area around Gothic which overlap extensively in flowering phenology and habitat. *Lathyrus leucanthus* and *Vicia americana* are different colors (white and magenta, respectively), and the former has a shorter corolla tube than the latter (8.77 mm vs. 12.42 mm). The same bee species can be found feeding on both flower species, but all the bees appear to prefer *Vicia*, the longer of the two flowers. This preference, also noted by G. Pyke and J. Pleasants (personal communication), would not be predicted on the basis of corolla tube length. The difference in visitation can apparently still be explained by the parameter of time per flower. Although the regression line for *Lathyrus* has the expected, negative slope (Table 1), indicating that time per flower decreases with increasing proboscis length, the times are much longer than would be predicted for a flower of that size. Lovell (1918) provides a possible explanation for the unexpected difference in handling times. He noted that flowers of *Lathyrus odoratus* are very rarely visited by bees and suggested that this could be related to the firm closure of the flower, which requires a "very powerful bee to depress the keel and obtain the nectar". *Lathyrus leucanthus* has the same appearance as *L. odoratus*, and is evidently also firmly closed.

The data presented in this and other studies indicate that proboscis length is an important determinant of the efficiency of nectar extraction during foraging by bumblebees, and in turn, of patterns of flower visitation. This evidence substantiates the validity of proboscis length as a morphological indicator (Inouye, 1977) and supports the conclusion that competition affects the morphology of bumblebee mouthparts and the coexistence of bumblebee species.

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