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Notes and Discussions

Field Measures of Flower Constancy in Bumblebees

ABSTRACT: A field method for conducting insect choice experiments shows that bumblebees in Rocky Mountain subalpine meadows are flower-constant to a limited extent when visiting superficially similar composite flower heads.

Despite an extensive literature, dating to Aristotle (Grant, 1950), species-constant behavior of flower-visiting bees is still a research problem for pollination ecologists. In the years since the great interest in flower constancy by Darwin and his contemporaries, recent contributions have been (1) tightening definitions so that "constancy" refers only to individuals, while other terms describe species characteristics [Faegri and van der Pijl, 1966, although Faegri and van der Pijl (1979) have reverted to a looser definition, now proposing "fidelity" for the concept discussed here]; (2) considering the reasons for constancy in terms of energetic constraints on foragers, selection for efficiency, sampling requirements and costs of learning new flowers (Heinrich, 1976, 1979; Pyke, 1978a, b; Laverty, 1978, and many others); and (3) considering the effects of constancy on plants, in empirical studies of gene flow (Levin, 1974) and in theoretical models of plant competition for pollinators (Levin and Anderson, 1970; Straw, 1972; Bobisud and Neuhaus, 1975; Thomson, 1975; Waser, 1978). All of these advances, however, elaborate the theoretical concept of constancy without improving the techniques for measuring it. Traditional techniques for the field study of pollinator constancy include direct observation of flower visit sequences (Clements and Long, 1923) and microscopic analysis of pollen loads (Betts, 1920; Brittain and Newton, 1933, 1934; Spencer-Booth, 1965). Both methods are unsuited for examining an individual's willingness to change flowers because they confound constancy by choice with passive constancy, which may occur when an animal making random choices enters a monospecific patch of flowers. If one is testing hypotheses regarding individual specialization in different situations, passive constancy is of little interest, but the strong tendency of flowering plants to form contagious distributions makes it an almost ubiquitous source of confusion.

A way to circumvent this difficulty is to consider only pollinator visits to a pair of flowers or inflorescences, which may be set up artificially, in water, at any desired spot. If the distance between the experimental flowers is small relative to the nearest other flowers, they may be considered equally accessible to visitors, and any significant departure from equality of visits, easily tested by a goodness-of-fit test, may be regarded as occurring by choice. The shortcomings of this method, which was used extensively by Clements and Long (1923), are the difficulty of obtaining enough visits to the experimental bouquet; the occasional difficulty of ascertaining the species which a forager was visiting before moving to the bouquet, which is necessary for measuring conditional transition probabilities, as used, for instance, in Straw's (1972) competition model; and the danger of bias due to repeated sampling of a few visitors which may be maintaining foraging locations around the bouquet.

A simple change eliminates both difficulties when working with pollinators which are tolerant of observers. The experimental bouquet is converted to a movable feast by presenting the flowers in an array of small vials of water at the end of a rod approximately 1 m long. The investigator can locate a suitable test subject in a suitable area, note its foraging pattern, and then present the bouquet; if desired, repeated presentations may be made until a response is recorded, or one individual may be scored repeatedly. The bouquet may comprise more than two species, and intrabouquet transitions may then also be scored, although their analysis is less straightforward than that of initial choices only. The greatly increased speed of this technique makes it possible for a single observer to obtain sufficiently large samples of rather rare events. While the suggested improvement seems a minor one, the increased quantity and quality of the data obtained per unit effort will be immediately appreciated by anyone comparing stationary and mobile bouquets in the field.

The following data, which indicate the usefulness of the technique, were gathered in a floristically rich subalpine meadow in the East River valley in Gunnison Co., Colorado, in 1977 (Thomson, 1978). When the measurements were taken, in early August, the primary food sources of the short- and medium-tongued bumblebees *Bombus silvicola*, *B. frigidus*, *B. occidentalis* and *B. flavifrons* were several species of yellow to yellow-orange Compositae which looked superficially similar and demanded roughly the same foraging techniques. As part of an investigation of plant competition for pollinators, I wished to determine the willingness with which bumblebee pollinators passed among these species. I used a bouquet of seven heads, and in most cases presented the bouquet to an individual bee more than once. The heads were positioned far enough apart that bees had to fly between them. I replaced the flowers with freshly picked ones at about 15-min intervals, and repositioned them within the bouquet, to avoid positional bias, at about 5-min intervals. The yellow composites used were *Arnica mollis, Senecio crassulus, Helenium hoopesii, Helianthella quinquenervis, Agoseris glauca* and *Chrysopsis villosa;* additionally, in one series, I included the pink ray-flowered *Erigeron peregrinus,* which was occasionally visited by bumblebees, although more frequented by solitary bees and flies. Table 1 presents data from 3 days' observations in a patch of *Chrysopsis villosa.* There were no significant differences among the four species of *Bombus,* and the data for nectar-foraging individuals of all species are pooled. All bees were foraging on *Chrysopsis* before moving to the bouquet; only the first flower visited in the bouquet is used for analysis. Visits were ignored if no probing occurred. Table 2 gives results from similar experiments in a patch of *Agoseris glauca.* The X^2 values given are based on an expectation of equal visits to each head in the bouquet. Preference indices are computed by dividing the observed by the expected number of visits for each species, then dividing this quotient for each species by the quotient for the "donor" species, *i.e.,* the one on which the bee was feeding prior to entering the

TABLE 1.—Analysis of moves from *Chrysopsis villosa* (CV) to bouquets containing CV, *Senecio crassulus* (SC), *Helenium hoopesii* (HH), *Arnica mollis* (AR), *Helianthella quinquenervis* (HQ), and *Erigeron peregrinus* (EP)

	Number of moves to: CV	SC	HH	AR	HQ	EP	
All moves							
Observed	60	8	10	12	8	1	$X^2 = 77.05$
Expected	23.4*	15.1	15.1	15.1	15.1	15.1	df = 5
Relative preference	1.000	.207	.259	.310	.207	.026	$p < .001$
Inconstant moves only							
Observed		8	10	12	8	1	$X^2 = 8.91$
Expected		7.8	7.8	7.8	7.8	7.8	df = 4, ns
Yellow-flowered species only							
Observed		8	10	12	8		$X^2 = 1.16$
Expected		9.5	9.5	9.5	9.5		df = 3, ns
Lumped yellow spp. vs. EP							$X^2 = 7.41$
Observed			38			1	df = 1
Expected			31.2			7.8	$p < .01$

*This expected value is larger than the others because some of the bouquets contained two heads of CV; this value takes into account the actual availability of CV during the series of observations

TABLE 2.—Analysis of moves from *Agoseris glauca* (AG) to bouquets containing AG, CV, SC, HH, HQ, AR, and EP (Abbreviations as in Table 1)

	Number of moves to: AG	CV	SC	HH	HQ	AR	EP	
All moves								
Observed	11	4	8	10	18	1	0	$X^2 = 32.3$
Expected	7.43	7.43	7.43	7.43	7.43	7.43	7.43	df = 6
Relative preference	1.000	.364	.727	.909	1.636	.091	.000	$p < .001$
Inconstant moves only								
Observed		4	8	10	18	1	0	$X^2 = 32.9$
Expected		6.83	6.83	6.83	6.83	6.83	6.83	df = 5
								$p < .001$
Yellow-flowered species only								
Observed		4	8	10	18	1		$X^2 = 20.5$
Expected		8.2	8.2	8.2	8.2	8.2		df = 4
								$p < .001$
Yellow spp. vs. EP								
Observed			40				1	$X^2 = 7.90$
Expected			32.8				8.2	df = 1
								$p < .01$

bouquet. Thus the preference for the donor species equals 1.0, and other species' preferences are expressed relative to that.

Flower choice by these bees is definitely not random (Table 1). Flower constancy exists in the form of a greater proportion of visits to *Chrysopsis villosa* than expected if random; there is also a significant tendency to visit yellow-flowered species instead of the pink *Erigeron peregrinus,* although there is no significant heterogeneity in frequencies of moves to yellow composites other than *Chrysopsis.* The indications of Table 2 are somewhat different: bees foraging on *Agoseris glauca* moved to *Helianthella quinquenervis* more often than remaining constant on *Agoseris,* although this difference is not significant (X^2 = 1.96, 1 df). There is significant heterogeneity in inconstant visits to yellow-flowered species attributable to an excess of visits to *Helianthella* and a deficit to *Arnica mollis. Erigeron* is again avoided.

No clear-cut explanation exists for the apparent difference between *Agoseris* and *Chrysopsis* bees in discrimination among yellow-flowered species. *Agoseris* heads are only visited during the morning, and different diel reward schedules by the other species could have contributed to the observed deviations from expectation, but I have no data on reward amounts or timing. The preponderance of *Agoseris* to *Helianthella* visits may be an effect of prior conditioning; the area where *Agoseris* grew, and these measures were taken, had been previously dominated by a dense bloom of *Helianthella.* The *Helianthella* bloom peaked 13 days before the *Agoseris,* and it was extremely attractive to bees. It is probable that some of the bees maintaining foraging areas in this part of the meadow had become accustomed to working *Helianthella* and still reacted to it as a preferred food source, while bees in the *Chrysopsis* areas were less likely to have foraged heavily on *Helianthella.*

These choice experiments corroborate earlier observations suggesting an intermediate level of constancy by bumblebees. Analyses of *Bombus* pollen loads in various situations have found the percentage of mixed loads to range from 31% (Colorado—Macior, 1974) to 51% (also Colorado—Clements and Long, 1923), with a mean of 44% for all the sources cited by T. Laverty (unpubl. review paper). Bumblebees are generally considered to be less constant than honeybees (whose mean percentage of mixed loads = 16% for the papers cited by Laverty), and their inconstancy apparently increases with local plant species diversity (Spencer-Booth, 1965). On the other hand, the percentage of foreign pollen in mixed loads is usually small (Macior, 1974), and although it is impossible to infer the probability of heterospecific visits from load data, the small percentages suggest that such visits might be rare. As mentioned earlier, such rarity may have active or passive origins.

The behavior of bees visiting the bouquets, taken together with the load data in the literature, suggests that both components are important in determining the patterns seen in the field. Active constancy, which transcends the spatial distribution of flowers, does exist in the bees as a whole as demonstrated by their behavior on the bouquets. However, it is far from complete, and almost all the individuals for which I recorded several bouquet visits made at least one visit to a different species. The bees which worked the bouquet, then, would have had a very high proportion of mixed loads, and the more moderate level of load-mixing seen in naturally foraging bees probably reflects passive constancy caused by foraging in largely homogeneous areas, as Spencer-Booth (1965) suggests. The patterns described are generally consonant with Heinrich's (1979) description of bumblebees foraging on a "major" and a "minor" plant species; however, this terminology may engender some confusion, since the repertoires of single bees in these experiments included several species. Observations of naturally foraging bees confirmed their willingness to forage actively from up to five species of similar flower heads in one foraging bout. It seems an arbitrary dichotomy to designate one of these "major" and the others "minor" when in fact they form a (probably continuous) rank order of preference.

It must be stressed that inconstancy need not imply inability to distinguish flowers. While these yellow composites may well be evolutionarily maintained in conformity to a common generalized "search image" of the bees (Thomson, 1978, 1980), they still probably provide sufficient cues, olfactory and visual, to allow their individual recognition, especially by insect sensory apparatus (P. Kevan, pers. comm.; Eisner *et al.,* 1969). Inconstancy may include some mistakes, but it is more satisfactorily explained as a positive element of an efficient resource harvesting and sampling program (Heinrich, 1979). The experimental bouquet technique, like artificial flower experiments (*e.g.,* Heinrich *et al.,* 1977; Hartling and Plowright, 1979), should be instrumental in placing this aspect of pollinator behavior firmly in its proper context of foraging theory. Additionally, it is well suited for examining the relative pollination status of flower variants within a species, *e.g.*, different sexes, sizes, scents, colors or style-morphs. It also may find application in unrelated questions involving field choices by tractable animals, *e.g.*, oviposition plant choice by butterflies.

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