THE TAXONOMIC DISCRIMINATION OF BEES

A. J. BATEMAN

The John Innes Horticultural Institution, Bayfordbury, Herts

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It has been known at least since Aristotle and repeatedly confirmed (see Grant, 1950) that hive bees tend to work one plant species at a time. This is in the interest of both plants and insects. For the plants it saves indiscriminant dissipation of pollen as in wind-pollinated species. For the insects their efficiency in the collection of nectar or pollen is doubtlessly increased if the manner of visiting flowers is standardised over long periods and the insect has not to be continually learning the best approach to a new species.

As a result of this relationship between plant and pollinator, differences in flower colour and form which are discernible to bees can play an important role in isolation between incipient species which as yet have no barriers to crossability other than the behaviour of their pollinators. The evolutionary significance of this relationship has been discussed by Grant (1949). Mather (1947) has argued that there will be a range of similarity between forms at and below the specific levels, over which the discrimination by the bees is absent or imperfectly developed. Under these conditions the degree of constancy of bees would be measurable by appropriate techniques.

It was to study this transitional phase in bee behaviour that the experiments about to be described were undertaken.

THE EXPERIMENT

Brassica napus (swede) is an allotetraploid hybrid between *B. oleracea* (cabbage) and *B. campestris* (turnip). Some of the main distinguishing features of the species are as follows :—

	<i>B. oleracea</i>	×	<i>B. campestris</i>	—→	<i>B. napus</i>
	n = 9		n = 10		n = 19
flowers	large		small		intermediate
pedicels	stout		slender		intermediate
corolla	pale yellow		bright yellow		bright yellow (type)
<i>Varieties used—</i>					
Green : aerial parts (excl. corolla) green					White-fleshed : bright yellow corolla
Red : aerial parts (excl. corolla) suffused with anthocyanin					Yellow-fleshed : dull yellow corolla

As has been previously observed (Bateman, 1947) bumble bees, which pollinate *B. oleracea* freely, never visit *B. campestris*. It was

inferred that the small flowers and pedicels of *B. campestris* caused bumble bees to avoid this species. The red colour in red cabbage is noticeably present even in the calyx, filaments and ovary. The particular green cabbage used had shorter plants at flowering time than the other three forms.

The experimental material consisted of 60 plants blooming in May 1949 and comprising 15 plants of each of the four types: red cabbage, green cabbage, yellow-fleshed swede and white-fleshed swede, arranged in random order. The activity of pollinating insects on this plot was observed on three days in May, the 4th, 6th and 13th. While several species of bee were observed on the plot they were classified into three classes only; bumble bee, hive bee and solitary bee. The total amount of data did not warrant any further subdivision.

A bee leaving a flower on a given plant is more likely to visit next another on the same plant than one on any other (*ibid.*). In an experiment such as the present, therefore, the only relevant observations are the plants which the bees visit on leaving one plant for another. It is only then that they are presented with a choice between forms.

While the main experiment was in progress, a short distance away were two larger plots in full bloom side by side, one of swede and one of cabbage. A survey of the insects visiting these plots gave the following figures.

	Hive bees	Bumble bees	Solitary bees
Swede . . .	68	0	4
Cabbage . . .	69	6	6

This gives the relative frequency of the three classes. The absence of bumble bees from the swede was confirmed by the detailed observations on the randomised plot. These are summarised in table 1.

INTERPRETATION

These observations are concerned with the discrimination of bees between plant forms. Such discrimination expresses itself in two ways. In the first way it appears as a preference for one of two forms when given free choice. It is not so easy, however, to measure such preference directly, because one can never be sure that there is equal freedom of choice between the species. Although the four varieties of *Brassica* used in this experiment were equally numerous, they varied in flower production. The green cabbage was definitely the least prolific in flowers and the swede varieties were most prolific.

Factors such as these, masking preference for a particular species

should, however, be the same for all insects. If we compare the distribution in *a*, *b* and *c* of table 1 it is evident that if we take hive bees as the norm (which does not imply that they show no preference),

TABLE 1

Pairs of consecutive plants visited classified by variety or species. Rows, first plant of the pair; columns, second plant of the pair. R G, Y W, C S represent red and green cabbage, yellow and white swede, cabbage and swede in that order

Pollinator	Hive bees				Bumble bees				Solitary bees			
No. of forages	26				12				8			
Total plants	301				98				53			
	R	G	Y	W	R	G	Y	W	R	G	Y	W
R	55	6	6	3	72	8	0	0	1	0	0	3
G	9	17	0	6	12	6	0	0	1	0	0	1
Y	4	0	51	33	0	0	0	0	0	0	7	7
W	5	5	29	72	0	0	0	0	1	2	7	23

	C	S
C	87	15
S	14	185

(a)

	C	S
C	98	0
S	0	0

(b)

	C	S
C	2	4
S	3	44

(c)

bumble bees visit only cabbage and solitary bees show a strong preference for swede. Flower size may well be the deciding factor, since hive bees are intermediate in size between bumble bees and solitary bees. The discrimination against both swedes and turnips by bumble bees is indeed very strong, for in much bee watching on these crops I have never seen a bumble bee on either species.

The second way in which discrimination between forms can be expressed is in flower constancy. This appears to be a basic instinct in bees, extending over all insect-pollinated flowering plants. It may not be determined directly by the ability of the bee to discern any difference between types, though the failure to detect constancy in respect of flower colour alone (*e.g.* Mather 1947) could be due to insufficiently sensitive tests. The bee may well give varying weight to different characters producing a sort of "discriminant function" by which its behaviour is determined.

Flower constancy is measured by observing the frequency with which a bee leaving a plant of class A and given an equal choice of classes A and B, continues to visit A. If the bee visits A and B with equal frequency the flower constancy is zero. If it visits A only the flower constancy is at a maximum, say unity. We have, therefore, to derive a measure of constancy which varies from 0-1. In practice,

however, the insect is not given an equal choice. Firstly, an insect leaving a plant of variety A has a choice of 14 other plants of variety A to 15 plants of any other variety. The bias introduced in this way is trivial in comparison with the error variation and in any case is bias in the safe direction, that is it reduces the apparent discrimination. Secondly, the varieties vary in their abundance of flowers as mentioned above. Finally, there is the above-mentioned preference from whose effect our index of constancy must if possible be kept free. In calculating the index of constancy we must therefore allow for the different frequencies in the two like-to-like classes of each 2×2 table. A similar problem is presented in calculations using linkage data in which both pairs of alleles have differential viability, and has been dealt with mathematically in general form by Fisher and Bailey (1949). The constancy data present a particularly simple case. If we represent our 2×2 table as follows:—

		2nd visit		
		A	B	
1st visit	A	a_1	a_2	
	B	a_3	a_4	with $a_1 + a_2 + a_3 + a_4 = n$

Then the best estimate,* or index, of constancy is

$$\frac{(a_1 a_4)^{\frac{1}{2}} - (a_2 a_3)^{\frac{1}{2}}}{(a_1 a_4)^{\frac{1}{2}} + (a_2 a_3)^{\frac{1}{2}}}$$

The test of significance of deviation of this expression from zero is given by the contingency χ^2 for one degree of freedom.

In this way we can calculate from the data in table 1A that the constancy of hive bees in respect of the species cabbage and swede is 0.795 with a χ^2 of 185.24. It remains a possibility that a spurious constancy could be obtained, if during the period of the observations the flowering of the two species was staggered, one species predominating at first and the other later. This is easily checked by taking the data for the three days separately as in table 2. There is highly significant constancy on each day.

* Bailey's estimate of the recombination fraction p from backcross linkage data, in our symbolism, is

$$\frac{(a_2 a_3)^{\frac{1}{2}}}{(a_1 a_4)^{\frac{1}{2}} + (a_2 a_3)^{\frac{1}{2}}}$$

and varies from 0 when linkage is complete to $\frac{1}{2}$ with no linkage. For our present use we require an expression that is 0 when $p = \frac{1}{2}$ (no constancy) and 1 when $p = 0$ (complete constancy). The index of constancy given here is a derivative of Bailey's formula with the required properties.

In spite of the strong avoidance of cabbage by solitary bees it is still possible to calculate their specific constancy. It is 0.457 with a χ^2 of 4.52 ($P = 0.04$). It may at first seem surprising that the

TABLE 2

Hive bee data presented separately for each day's observations

Date in May	4th	6th	15th
	C S	C S	C S
C	34 12	6 1	47 2
S	12 124	0 22	2 39
$\chi^2_{[1]}$	77.11	23.78	74.60

constancy is less than for hive bees which show much less preference. The above index takes into account, however, not only the fidelity to swede of insects pollinating swede but the fidelity to cabbage of insects pollinating cabbage. If solitary bees avoid cabbage even when they have just been pollinating it they will thereby lower their index of constancy.

Analysis of the data discloses discrimination also between varieties of the same species though rather weaker, as might be expected, than that between species. All calculable indices with their respective χ^2 's are shown in table 3. The lower χ^2 's for bumble and solitary bees

TABLE 3

Constancy indices for the three classes of bee for all visible comparisons

	Hive bees		Bumble bees		Solitary bees	
	Index	χ^2	Index	χ^2	Index	χ^2
C—S	0.795	185.24			0.457	4.52 ²
R—G	0.615	28.92	0.359	6.53 ¹		
Y—W	0.325	19.14			0.289	3.13 ¹

¹ $P = 0.01$

² $P = 0.04$

³ $P = 0.09$

arise as much from the smaller numbers of observations as from the lower values of the index.

The discrimination between varieties is of some evolutionary significance since it shows how normal intra-specific variation can act as a stimulus to isolation by affecting bee behaviour. This in turn would increase the rate of divergence which would increase the bees' discriminatory powers. The lower constancy indices of bumble and solitary bees confirm observations of other workers (*vide* Grant, 1950).

One curious feature of the 4×4 table in table 1A is the apparently complete isolation between green cabbage and yellow swede. This may be a fortuitous result of the rather low numbers involved. (The

FIG.—Details of nine forages of hive bees visiting both species. x = a cabbage plant, o = a swede plant. Read from left to right. At extreme right is the total number of plants per forage. Besides those illustrated there were eight forages confined to cabbage, comprising :

4, 6, 7, 7, 10, 11, 19 and 22 plants

and nine forages confined to swede, comprising :

6, 7, 8, 10, 10, 14, 19, 22 and 30 plants.

frequencies of the comparable like $\times$ unlike crosses vary from 6 to 3.) On the other hand it may arise as an interaction between varietal characters. The green cabbage was distinct from the other three forms in plant height. The yellow swede was distinct from the rest

in flower colour. The two characters together might have reinforced the normal interspecific discrimination to give a greater discrimination than between any other pair of varieties.

Since the data were collected forage by forage it is possible to test for heterogeneity between forages (which is probably a measure of heterogeneity between bees) and to observe the precise sequence of visits in any one forage. Only the hive bee data are considered here since they were most extensive. Those forages involving crossing between species are presented in detail in fig. 1. Those confined to one species need be represented merely by the number of plants visited. The varieties have been ignored since they would have made the diagrams too complicated.

Owing to the variable sizes of the forages a statistical test of heterogeneity is out of the question. However some conclusions can be drawn from a superficial survey. Out of 26 forages, containing 29 instances of crossing from one species to another, an average of just over one per forage, 17 are confined to one species and only 9 are mixed. Of these 9, one, no larger than several pure forages, contains 11 crossings. Clearly there is heterogeneity between forages. This may be due to congenital differences in the bees, or to environmental factors such as age of the individual. By analogy with territorial fixation (Butler, 1945) it would appear possible that the more erratic forages are those of younger bees. In any case the immediate cause of inconstancy might be inadequate powers of discrimination.

Inspection of the mixed forages enables us to test this possibility. In all but three there is a tendency for the bee to pay most attention to one species, the visits to the second species being aberrations which are never continued for more than one plant at a time. This rather points to the lack of fixation being due to poorly developed powers of discrimination rather than indifference to which species is being worked. In the three exceptions apparently showing a switch in mid-forage from one species to the other the period on the first species is only two or three visits, possibly at the start of a forage, before the conditioned reflexes had got running smoothly. One minor feature of the data is that in all the mixed forages save one the main species is swede with aberrant visits to cabbage. In the three showing a switch, the switch is from cabbage to swede. This is very suggestive that the bees have a real preference for swede and it is only the strong species constancy of those bees working cabbage which keeps them on that species.

Tests have also been made for heterogeneity between forages in constancy to varieties. One might expect any such heterogeneity to be correlated with that found in specific constancy. If we calculate separately the constancy indices between swede varieties according to whether the bees show or do not show complete species constancy (data in table 4) we get very marked heterogeneity. Bees constant to swede have an intervarietal index of 0.402 and a χ^2 of 18.89.

Bees working both species have an index of only 1.135 with a non-significant χ^2 ($1.06 = P$ of 0.3). Unfortunately a similar comparison

TABLE 4
Comparison of the constancy to swede varieties of hive bees grouped according to their species constancy

	Bees visiting swede only		Bees visiting both species	
	Y	W	Y	W
Y	41	18	10	15
W	17	41	12	31
Total plants	117		68	
χ^2	18.89		1.06 ($P = 0.3$)	
Index	0.402		0.135	

cannot be made using cabbage varieties because the bees working both species rarely worked two cabbage plants consecutively.

SUMMARY

Observations were made on bees foraging on a randomised plot consisting of equal numbers of two cabbage and two swede varieties.

Hive bees visit both species with about equal frequency, bumble bees visit only cabbage, while solitary bees concern themselves mainly with swede.

Hive bees show, at least within forages, a high but incomplete constancy to species and a lower but still highly significant constancy to varieties within a species. Wherever comparisons are possible the constancy of bumble bees and solitary bees is weaker than that of hive bees.

Examination of separate forages shows marked heterogeneity in degree of discrimination expressed both between species and between varieties. There is a correlation between interspecific and intervarietal discrimination.

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