Some Observations on Scents among Bees and Wasps (Hymenoptera).

By

BERTIL KULLENBERG.

Zoological Institute of Uppsala University.

Practically nothing is known about the many types of scent substances occurring among insects, which play an important part in their sexual attraction, says Lederer in his particularly interesting and fascinating work, *Odeurs et Parfums des Animaux*. It has been known for a long time that many insects have characteristic scents. Wigglesworth has given a general account of the extreme and diverse importance of scents in the insect world. The unpleasant odour from the flour beetles *(Tribolium)* is probably well-known to many people. The odour has a toxic effect on other insects. However, not all insect scents are unpleasant to humans. The author has described a number of scents from the capsid bugs which are often pleasant and sometimes reminiscent of fruit.

There is a variety of perfumes produced by the hymenoptera, and in many cases these are easily detectable to the human sense of smell, often being pleasant scents for us. Most entomologists have probably observed that the small bees of the genus *Prosopis (Hylaeus)* have a strong scent like lemon or melissa oil. The French zoologist F. Bernard describes the scent of the *Colletes* bees as similar to sugar-candy or Reseda, and that of the *Prosopis* bees as like citronelle, Geranium, Verbena or bedbugs.

The author observed that the flowers of the genus of orchids, *Ophrys*, secrete scents which have the effect of sexual attractants on certain male hymenoptera, and it seemed important to determine and describe the scents of as many hymenoptera as possible. The nose must be used for the analysis, and the scents have to be compared with known odours in describing them. Technical development has not yet advanced to such a stage that it is an easy matter to carry out a chemical analysis of quantities as small as those in question here. The excellent work of W. Jacobs indicates where we should look for the scent-producing organs on the bodies of the hymenoptera.

The following table gives a short summary of the results hitherto obtained in a study of the scents of several species of hymenoptera in Sweden. Species names are not given, except for a few particularly interesting cases. In many cases, progress has so far been made only in the study of one specimen. The types of scent are also generalised to some extent, since some of the finer gradations which have seemed to be detectable cannot be published at the present stage of the investigations. The table gives an account of the available material, but it is advisable to append some comments.

The different types of scent mentioned (21 of them) thus constitute a simplified version of the complete range of types which I think I have detected. The account is a generalisation which is sometimes not a very good description of the actual observations. For instance, *Crabro* is given as having a scent like farnesol as well as one like lemons. I have detected a scent from one of the species of his genus which is sweetish, and usually rather like that of farnesol or nerolidol. But there was also a definite, though faint, secondary scent of citron or citronellol, which has not been included in the table. It has the effect of accentuating the farnesolic scent to some extent, so that it becomes like what might be described as »newly-washed linen». I have been able to imitate this scent by adding a little citronellal to farnesol. There was also a detectable scent of the lemon-farnesolic kind from bees of the genus *Andrena* (solitary bees).

It is difficult to describe scent no. 7, and sometimes all the tones occur with the same individual. No. 10 is a scent like a mixture of powdered coffee and cocoa, very similar to that which is characteristic of »Nescafé». No. 15, »young leaves or buds of birch and hazel», is the type of scent which I have found most frequently among species of *Crabro* and certain bees. The odour is like »cloudy» farnesol. with a slight addition of a lemon scent. Sometimes it is like the odour of so-called cyclamen aldehyde, or to some extent like the scent of cultivated *Cyclamen*. I have been able to make a fair imitation of the scent by adding a little butyric acid and citronellal to farnesol, but the basic element is a pleasant, rather sweet smell like that of nerolidol or farnesol. No. 14 is a similar sort of mixed scent. A lemon scent also occurs in no. 20, with a very faint secondary vanilla note.

It is noticeable that bees (Apidae) and digger wasps (Sphecidae) exhibit similar types of scent for the whole family: on the one hand scents like lemon or farnesol, and on the other scents like garlic, bread, rabbit hutch—crab—wet wool. The ichneumonids which I have referred to have similar types of scent.

It is interesting that among domestic bees the Italian breed has a scent like geraniol or citronellol, while the Nordic and Krain breeds have a scent like bananas (at least, in southern Sweden). Up to now, it has only been possible to observe scents in the case of workers.

	Number of species	Number of individuals	Types of scent																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
Sphecidae																							
Oxybelus	1	1								1													
Crabro	3	11															2	5	10				
Cerceris	1	2																2					
Tachysphex	1	2							1	1									1				
Mellinus	1	3												3					3				
Nysson	1	m	1				1					m											
Gorytes.....	4	m				1					m	m			m	2		1	5				
Microphus.....	1	1	1																				
Apidae																							
Prosopis	2	2																2					
Colletes	1	3																	3				
Halictus.....	5	16	14				1											1					
H. calceatus ...	1	m					1																m
Sphecodes	3	3	3																				
Eriades	1	2														2		2					
Osmia	5	25	14														7		4				
Stelis	1	1								1													
Megachile	1	2								2								1					
Andrena	14	60	6				30	2	6	2								20	6	1		1	
A. nigroaënea ..	1	23	6						1											17			
Nomada.....	3	5	2		3													1					
Dasypoda	1	2	1																1				
Macropis labiata	1	m				m			m										m				
Eucera.....	1	5	1							1							4				1		
Anthophora....	2	6	3														3		1				
Bombus	3	m				m											1	1	m				
Psithyrus.....	1	m				m													m				
Apis mellifica (Nord.)	1	m																		m			
Apis mellifica (Ital.)	1	m																m					
Chrysididae																							
Chrysis	3	3					2	1	1														
Mutillidae																							
Mutilla	1	1									1	1											
Vespidae solitaria	4	4						1				4											
Ichneumonidae	7	9		1		4	1						1				2		5				

m = many tested individuals.

Odours: 1 not perceptible, 2 allyl alcohol, 3 formic acid, 4 butyric and valerianic acid, 5 garlic, 6 cream, 7 rabbit hutch, crab, wet wool, 8 bread, 9 green odour, 10 coffee, cocoa, 11 caraway, 12 ethyl acetate, 13 benzaldehyde, 14 film celluloid or cigar-box, 15 young leaves or buds of birch or hazel, 16 citronellol—geraniol—citral, 17 farnesolic—flowery, 18 banana, 19 Dolycoris bug, 20 citronellol + vanillin, 21 like muscone.

From the biological point of view, the question of the function of these scents is an interesting one. Observations of insects in the wild state led me some time ago to the idea that scent plays an important part in stimulating the copulatory attack of the male, as well as the search for the female — at least, as far as attraction at close quarters is concerned. I have observed that certain species of the orchid genus *Ophrys* give off an odour which acts as a sexual attractant and sexual excitant for the males of certain bees and digger wasps. I found that the scent of one of these orchids was like that from the female counterpart of the male wasp which was attracted by it and effected the pollination. Males of *Gorytes campestris* L. (a digger wasp or sphecid) were observed to give off a fine, clearly perceptible »flowery» smell while swarming in a sand-pit well-shielded from air currents. On a few occasions, I have detected a faint »flowery» scent from swarms of proctotrupids (minute parasitic wasps) ; on catching one of them in the hand, quite a strong scent was observable. The strongest component of this scent resembled indol, although there was a »flowery» subsidiary scent like farnesol, giving a resultant scent described as »young hazel leaves» or »cigar-box».

The males and females of the hymenoptera appear to have the same scent, although it is usually weaker in the case of the males.

As the observations indicated that the scents act as »releasers» in mating, it was decided to undertake a large-scale systematic investigation concerning the chemical nature of substances which act as sexual attractants and excitants among aculeate hymenoptera. I started with substances having scents similar to those I had observed in connection with the sexual activity of these insects. I also applied my observations of the scents of *Ophrys* flowers. I have since begun to study other types of scent, and have made observations and experiments with other scent substances. A large range of such substances is needed for systematic investigations in this field. It is important to find out the significance of the molecular structure for sexual attraction and excitation, and whether there may be confusion of scent in connection with sexual attraction.

I now know the different mating stimulants for many species. All important stimuli other than scent were kept unchanged during these experiments. The bait used was either dead dry females or males, or rectangular pieces of cloth or paper of suitable size and shape, all of which had been tested beforehand. The perfumes were applied to the bait in concentrations judged to be equal to the strongest I had observed for the respective species; up to now, I have only experimented with changes of concentration in a few cases.

Substances acting as sexual attractants for males of the sphecid *Crabro cribrarius* L. were allyl alcohol, benzaldehyde, rhodinol, geraniol, citronellol, nerolidol, farnesol, citronellal, hydroxycitronellal, the

scent from flowers of *Ophrys insectifera,* and the farnesol-like scent from the female. Only the scent of the female had any considerable effect as an excitant, but there was some such effect from citronellal, hydroxycitronellal and the *Ophrys* scent used. Farnesol and nerolidol were occasionally excitant to some extent. But none of these perfumes had sufficient excitant effect to bring about copulation attempts, neither with dead females nor with pieces of cloth. Allyl alcohol and benzaldehyde apparently do not attract when used in stronger concentrations. Caprinic acid and caprylic acid have a repellent effect, while butyric acid is perhaps in certain concentrations a boundary case between attractant and repellent. It seems that a good attractant can overcome the effect of a repellent when it comes to the actual mating.

The bee *Macropis labiata* Panz. responded to the following as sexual attractants, arranged in ascending order of effectiveness: citronellol (?), citronellal (?), methyl pelargonate, farnesal, undecalactone, nerolidol, farnesol, the scent of the female. The attractant scent of the female of this species resembles farnesol in low concentrations, or better, undecalactone (peach aldehyde) with the suggestion of a fruity scent (apple-pieces in red-currant puré!). Only nerolidol, farnesol and the scent of the female had any excitant effect, and the males could not distinguish with certainty between farnesol and the female scent when the two scents were of the same strength. The difference between the attractive effects of farnesol and farnesal was considerable; and when farnesol or nerolidol were subject to too much sun or heat in the open air, so that they acquired a scent resembling farnesal (cf. Simonsen and Barton 1952), their attractive effect diminished. It was easy to bring about persistent attempts on the part of the males of this species to copulate with rectangular pieces of velvet — when the velvet surface was upwards. Farnesol and phenylethyl alcohol acted as sexual attractants and excitants for males of *Bombus lapidarius* L., while butyric acid and valerianic acid repelled males from mating when these substances gave off a scent at least as strong as they sometimes appear to do from the females.

My investigations would obviously be on a surer ground if some of the scents of the hymenoptera were chemically known. As it is, the identification of the scents is at present largely hypothetical. I wish to study the biological significance of scents among hymenoptera from both the interspecific point of view and the intraspecific, paying particular attention to the part they play in sexual activity, and if certain types of scent among these insects could be identified, the tests could from the beginning be put on another basis than hit-or-miss testing of suggested compounds.

It has already been mentioned that it is also desirable to study the connection between the sexual attractant and sexual excitant effects and the molecular structure of the substances concerned. Possible repel-

lent scents given off by the female are also under consideration. This would throw some light on the part played by scent stimulation in one aspect of the instinct life of the hymenoptera. It will be seen that certain scents secreted by the hymenoptera — and probably the same applies to other insects — act as sexual excitants in a way reminiscent of hormones. Since the scents are produced by the insects themselves, perhaps they might be called »parahormones»! Their effect, and that of certain known substances such as farnesol, nerolidol and citronellal in the cases referred to here, seems to be similar to that of muscone among some mammals. Scent is particularly interesting as a factor confining sexual activity to the species, particularly as the visual and tactile stimulation of mating instincts do not serve as especially good limiting factors in the male's choice of an object to mate with. I think that scent does in this respect contribute something to the biological isolation of the species, races or varieties. This brings us to the question of the importance of this study for problems associated with natural selection and evolution. Since it is possible to conceive of an immense number of possible experiments with various concentrations and choices of scents, covering a wide range with respect to chemical nature and type of scent, from the theoretical point of view it is clear that there is considerable scope for discussion of the importance of variability in scent production for natural selection.

In conclusion, it may be mentioned that the programme of investigation includes a study of the importance of scent for the female's orientation with regard to the nest, as well as the orientation of parasitic hymenoptera with regard to a particular species. It would also be of value to find out something about whether the parasite can achieve relative security by producing a scent which is either attractive or repellent for the host.

The evidence which we already have about the important part played by scent secretion in both intraspecific and interspecific relations among the hymenoptera indicates that it should be possible to arrive at a more or less correct understanding of whether the secretion of scent must be regarded as a real a d a p t a t i o n, or whether it merely depends on the metabolism and is evolved independently of the environment, by means of suitable field observations and experiments. It is also likely that some light will be thrown on the part played by scent in the attraction of insects to flowers and the pollinisation of entomogamous flowers, since many of the experiments employ substances which also occur in the scents of flowers.

Literature.

Bernard, F. (1951): Superfamille des Apoidea ou Abeilles. Traité de Zoologie X: 2.

Dethier, V. (1947): Chemical insect attractants and repellents. Philadelphia—Toronto.

Jacobs, W. (1924): Das Duftorgan von Apis mellifica und ähnliche Hautdrüsenorgane sozialer und solitärer Apiden. Zeitschr. für Morph. und Oekol. der Tiere 3.
Kullenberg, B. (1944): Studien über die Biologie der Capsiden. Zoologiska Bidrag från Uppsala, vol. 23.
—— (1951): Investigations on the pollination of Ophrys species. Oikos I: 2.
—— (1952): Recherches sur la biologie florale des Ophrys. Bull. Soc. Hist. nat. Afrique du Nord, 43.
Lederer, E. (1950): Odeurs et parfums des animaux. Fortschritte der Chemie organischer Naturstoffe 6.
Simonsen, J. and Barton, D. H. R. (1952): The terpenes, vol. 3. Cambridge.
Wigglesworth, V. B. (1950): The principles of insect physiology.