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The effect of social interactions on the production of mandubular gland signals in female african honeybees (apis mellifera adansoni)

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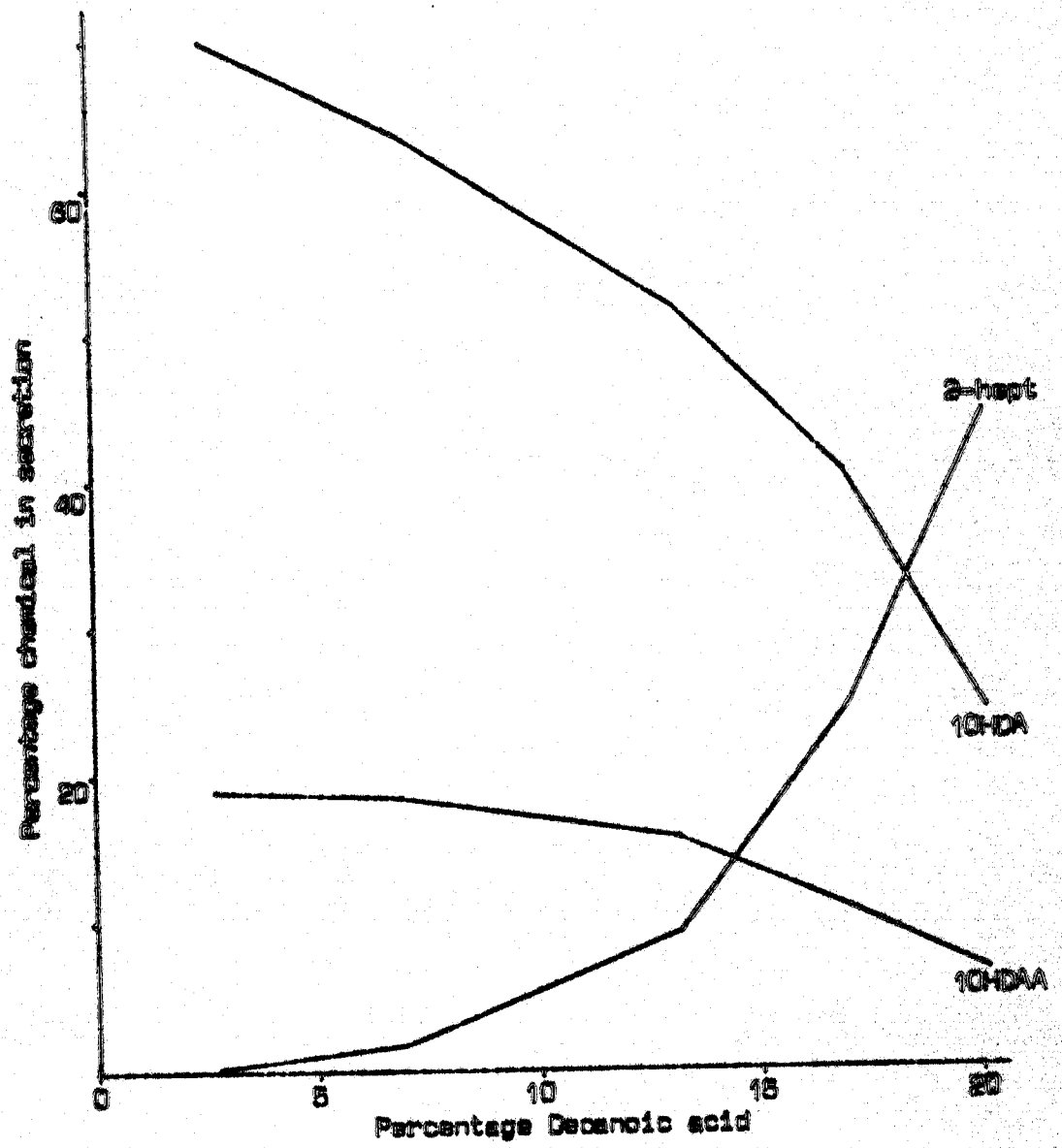


Figure 3.12. Relationship of 10HDA, 10HDAA and 2-heptanone to DAA in head extracts of queenless A.m.adansonii workers (queenless period two months)

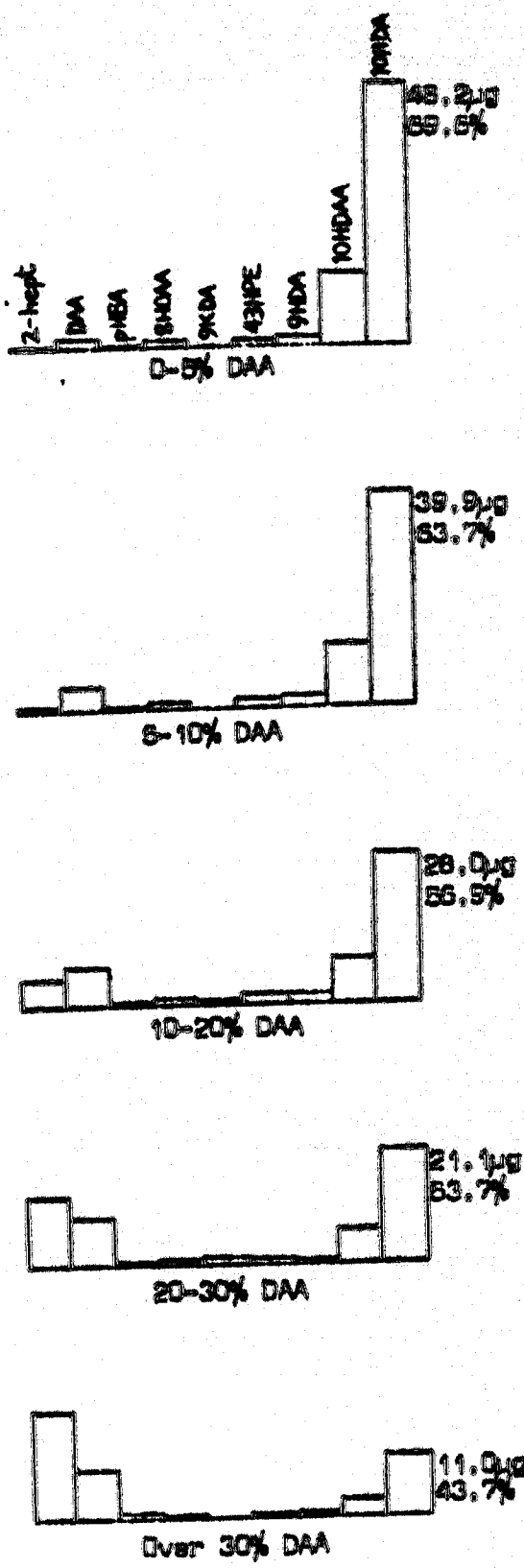


Figure 3.13. Relationship between DAA and eight other chemicals found in head extracts of queenless A.m.adansonii workers

Table 3.15. Relationship between proportions of DAA, 10HDAA, 10HDA and 2-heptanone in head extracts of groups of queenless A.m.adansonii workers and the degree of ovarial development (November 1979). Determined from Appendix Table 5

Ovarial development	Percentage chemical in secretion			
	DAA	10HDAA	10HDA	2-heptanone
0	14.1	11.0	35.4	34.1
1	13.7	13.1	44.5	21.8
2	7.8	17.1	57.3	9.8
3	10.0	16.6	61.9	3.7
4	8.8	18.8	60.9	0.9

Table 3.16. Relationship of 10HDAA, 10HDA and 2-heptanone to DAA in head extracts of groups of A.m.adansonii workers regardless of ovarial development (November 1979). Determined fr . Appendix Table 5

Percentage DAA in secretion	Percentage other chemical		
	10HDAA	10HDA	2-heptanone
2.8	19.4	70.2	0.3
7.0	18.6	63.4	1.8
13.3	15.7	51.8	9.4
17.2	11.1	40.3	28.2
20.4	6.6	24.2	44.6

Table 3.17. Relationship between the amounts of DAA and eight other chemicals in head extracts of groups of queenless A.m.adansonii workers (November 1979) (mean ± S.E.) Raw data Appendix Table 5

DAA levels	Ovarial development	Mean no. ovarioles	Total chemical (µg/head)									
			DAA	pHBA	8HDAA	9KDA	4OHPE	9HDA	10HDAA	10HDA	Total	2-heptanone
5%	1.2	3.3	1.9±0.32	0.2±0.13	1.4±0.43		1.6±0.40	1.9±0.45	13.3±1.51	48.2±7.38	68.5±9.57	0.2±0.18
5-10%	2.5	2.7	4.4±0.63	0.7±0.15	1.4±0.27	0.02±0.01	1.7±0.39	1.8±0.28	11.7±0.93	39.9±5.20	61.6±7.08	1.0±0.37
10-20%	2.0	2.6	7.2±0.68	0.5±0.15	1.4±0.32	0.12±0.05	1.6±0.31	1.6±0.25	8.5±0.87	28.0±2.57	48.9±4.52	5.1±1.45
20-35%	1.5	2.8	9.0±0.82	0.6±0.15	0.7±0.31	0.13±0.12	1.1±0.32	0.9±0.30	5.8±0.63	21.1±2.34	39.3±3.92	13.2±2.50
35%	1.0	2.8	9.3±1.38	0.7±0.23	0.3±0.11		0.5±0.21	0.5±0.19	3.0±0.46	11.0±1.39	25.3±3.03	20.3±3.80

Table 3.18. Relationship between the percentage of DAA and seven other chemicals in head extracts of groups of queenless A.m.adansonii workers (November 1979) (mean ± S.E.) Raw data Appendix Table 6

DAA levels	Ovarial development	Mean no. ovarioles	Percentage chemical							
			DAA	pHBA	8HDAA	9KDA	4OHPE	9HDA	10HDAA	10HDA
5%	1.2	3.3	2.9 ± 0.29	0.3 ± 0.14	2.0 ± 0.56		2.0 ± 0.46	2.5 ± 0.44	20.7 ± 1.25	69.6 ± 1.77
5-10%	2.5	2.7	6.9 ± 0.33	1.2 ± 0.30	2.2 ± 0.32	0.02 ± 0.01	2.6 ± 0.57	2.9 ± 0.28	20.4 ± 1.08	63.7 ± 1.61
10-20%	2.0	2.6	15.0 ± 0.83	1.0 ± 0.28	2.7 ± 0.53	0.22 ± 0.12	3.5 ± 0.79	3.1 ± 0.34	17.7 ± 0.65	55.9 ± 1.63
20-35%	1.5	2.6	23.3 ± 0.72	1.5 ± 0.89	1.8 ± 0.82	0.15 ± 0.12	2.4 ± 0.87	2.1 ± 0.58	15.1 ± 0.70	53.7 ± 1.91
35%	1.0	2.8	38.6 ± 1.88	2.6 ± 0.91	1.4 ± 0.61		2.0 ± 0.75	1.8 ± 0.62	11.9 ± 0.76	43.7 ± 2.52

their secretions were more queenlike. Instead all three were found to be subordinate to others in their group (their average social index being only 0.58) and somewhat inactive socially (averaging only twenty nine interactions during the study period compared with an average of fifty one interactions per bee among other individuals of similar age).(Appendix Table 7).

It was also thought, at the onset of this study, that dominant individuals would probably be more active socially, and there was evidence to indicate that this may be so. In seven of nine groups (the data of group 2 was excluded as all the bees of this group died by the seventh day) the most active individual had the highest or second highest social index. Howeve[illegible]ee occasions, dominant individuals were the least active (Grou[illegible]nd 9), and in Group 1 the most active individual was the least domin[illegible] member. This worker was one of the three individuals found to be secreting 9KDA (Appendix Table 7).

Number of ovarioles in the ovaries of A.m. adansonii workers and ovarial development during queenlessness

During the study, numbers of ovarioles in the ovaries of four samples of A.m. adansonii workers were counted and compared (Table 3.19). Four hundred and nineteen ovaries were assessed and the average number of ovarioles per ovary was found to be 3.69. A highly significant difference in the number of ovarioles per ovary was found between the bees sampled in November 1979 (mandibular gland analysis on page 64) and the other groups, two of which were sampled in February 1979 (mandibular gland analysis of both not done) and the third in February 1980 (analysis on page 125). While two of the February samples were significantly different, neither was significantly different from the third sample (Table 3.20). The mean number of ovarioles found in the ovaries of the February samples were 4.01, 4.36 and 4.86, while the workers examined in November had only 2.88 ovarioles per ovary. The ovaries of this group were reduced to such a degree that in eleven instances ovarioles were present only as minute filaments (none having developed germaria) a situation found in only one bee dissected in February. In addition only one ovary dissected in the November sample had more than seven ovarioles, while seventeen dissected in the February samples had more than seven, the largest of which consisted of twelve ovarioles.

Of the bees dissected, 58 per cent were found to have ovaries with

Table 3.19. The number of ovarioles in ovaries of *A. m. adansonii* workers of different colonies

Number of ovarioles	Groups of bees examined					
	Nov 1979	Feb 1979a	Feb 1979b	Feb 1980	Feb mean	Overall mean
0	11			1	1	12
1	34	7	1	2	10	44
2	37	13	4	7	24	61
3	45	25	5	12	42	87
4	44	11	13	21	45	89
5	21	15	4	21	40	61
6	5	10	2	12	24	29
7	2	4		12	16	18
8	1	5	2	1	8	9
9				5	5	5
10		1	2		3	3
11						
12				1	1	1
Ovaries assessed	200	91	33	95	219	419
Ovarioles per ovary	2.880	4.011	4.364	4.853	4.434	3.692
Poisson X^2 fit	.3 > P > .2	.5 > P > .3	.2 > P > .1	.7 > P > .5	.95 > P > .9	.5 > P > .3
Estimated variance*	0.014	0.044	0.132	0.051	0.020	0.009
S.E. (mean)	0.120	0.210	0.364	0.225	0.142	0.094
± 95% limits	0.24	0.41	0.71	0.44	0.28	0.18

* Using central limit theorem (estimated variance = s^2/n) as n is large

Table 3.20. Comparisons between the number of ovarioles per ovary in four colonies of A.m. adansonii workers

Comparison	D.F.	u-test[a]
Nov. 1979 v Feb. 1979a	289	8.35**
Nov. 1979 v Feb. 1979b	231	4.68**
Nov. 1979 v Feb. 1980	293	3.88**
Nov. 1979 v Feb. mean	417	7.74**
Feb. 1979a v Feb. 1979b	122	0.84N.S.
Feb. 1979a v Feb. 1980	184	2.76**
Feb. 1979b v Feb. 1980	126	1.17N.S.

Nov. 1979	Feb. 1979a	Feb. 1979b	Feb. 1980	
2.880	4.011	4.364	4.863	Means

(underlined means not significantly different)

[a] Using central limit theorem $\bar{x}/n = s^2/n$ therefore $u = \dfrac{\bar{x}_2 - \bar{x}_1}{\sqrt{\frac{\bar{x}_2}{n_2} + \frac{\bar{x}_1}{n_1}}}$

an equal number of ovarioles, or a difference of only one. In contrast, 13 per cent were found to have a difference of four or more, the largest difference being seven (Table 3.21). Differences in the number of ovarioles between left and right side ovaries were not found to be significant (Table 3.22). Relationships between the number of ovarioles and ovarial development were investigated in the November 1979 sample only (Table 3.23). It was found that ovaries with no development had significantly fewer ovarioles than did ovaries that had developed. In addition, ovaries that had developed to degree '1' had significantly fewer ovarioles than degrees '3' and '4'. Although differences between degrees '2', '3' and '4' were statistically insignificant, it appears that there is a trend for ovarial development to occur more readily, or more fully, in ovaries with greater numbers of ovarioles (Figure 3.14 and Table 3.24).

It was also found that the left and right side ovaries did not necessarily undergo equal development, although equal development had occurred in 51 per cent of the bees dissected. Thirty five per cent had ovaries whose development differed by one degree of development, 7 per cent by two degrees, 6 per cent by three degrees and one individual was found to have one entirely inactive ovary and the other with fully developed eggs. While differences in development between the ovaries of an individual did occur, development did not occur more frequently on one side than the other.

The bees dissected in this sample had been queenless for a period

Table 3.21. Differences in the number of ovarioles between the ovaries of individual A.m.adansonii workers

Ovariole difference between left and right ovaries	Percentage distribution of differences in ovariole numbers					
	Nov 1979	Feb 1979a	Feb 1979b	Feb 1980	Feb mean	Overall mean
0	20	27	31	17	25	26
1	28	27	38	37	34	32
2	23	13	19	26	19	20
3	12	11	12	9	11	11
4+	8	22		11	11	13

Table 3.22. Differences in the number of ovarioles between left and right ovaries in A.m.adansonii workers

Ovary	Mean number of ovarioles / ovary					
	Nov 1979	Feb 1979a	Feb 1979b	Feb 1980	Feb mean	Overall mean
Left	3.11	4.04	4.38	4.68	4.37	3.77
Right	2.66	3.98	4.35	5.04	4.46	3.61
Difference	0.45 (N.S.)	0.06 (N.S.)	0.03 (N.S.)	0.36 (N.S.)	0.09 (N.S.)	0.16 (N.S.)

Table 3.23. Relationship between the number of ovarioles and ovarial development in queenless A.m.adamsondi workers (November 1979)

Ovarioles per ovary	Stages of ovarial development				
	0	1	2	3	4
0	11				
1	12	8	8	7	
2	4	11	11	9	2
3	8	11	11	12	3
4	2	4	11	22	5
5	2	2	6	10	2
6			2	2	1
7				2	
8			1		
Ovaries assessed	39	36	50	64	13
Mean no. ovarioles	1.590	2.472	3.140	3.516	3.769
Poisson X^2 fit	.2 > P > .1	.3 > P > .2	.7 > P > .5	.1 > P > .05	.5 > P > .3
Estimated variance	0.041	0.069	0.063	0.055	0.290
S.E.(mean)	0.202	0.262	0.251	0.234	0.538
± 95% limits	0.40	0.52	0.50	0.46	0.17

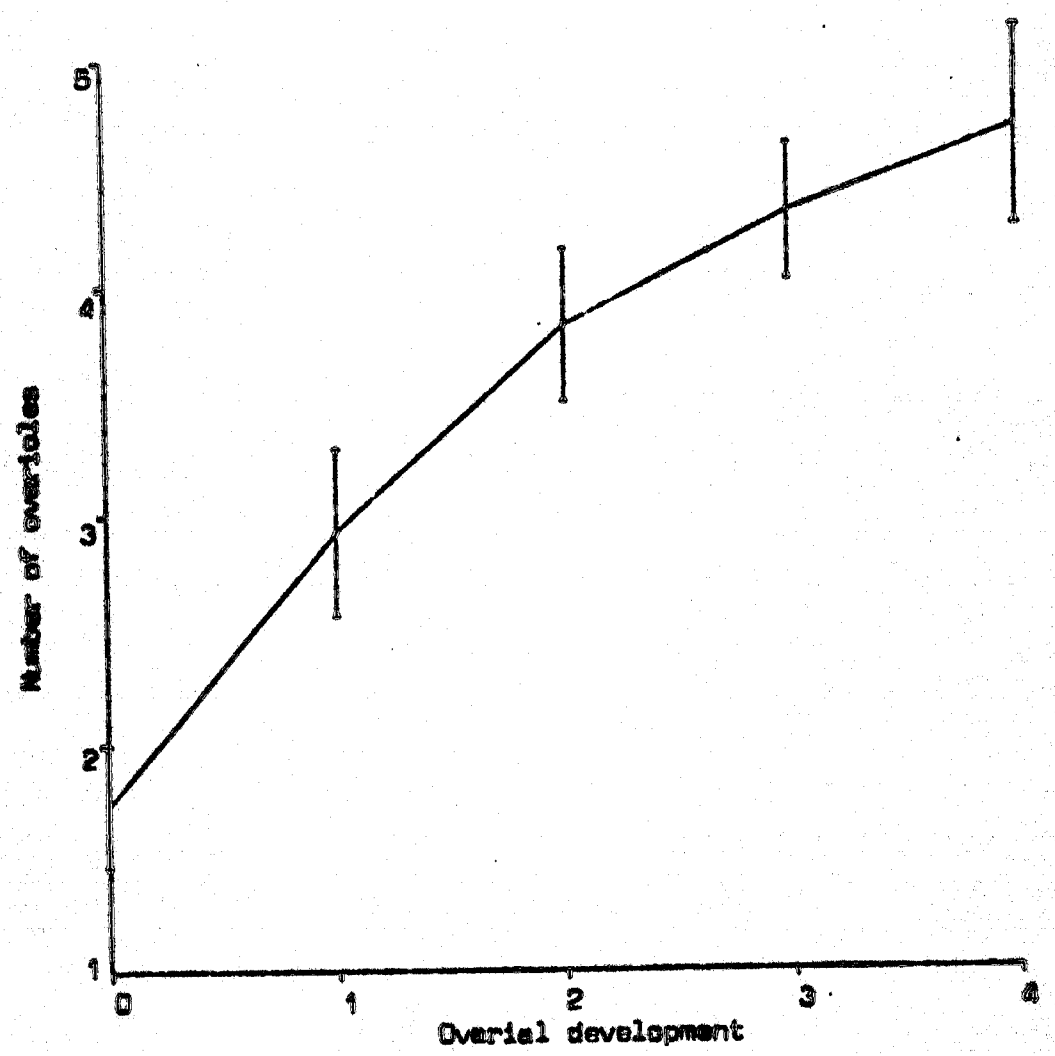


Figure 3.14. Relationship between the number of ovarioles and ovarial development in queenless A.m.adansonii workers

Table 3.24. Differences in the number of ovarioles of ovaries with different degrees of ovarial development

Comparison	D.F.	u-test[a]
'0' v '1'	73	2.67**
'0' v '2'	87	4.82**
'0' v '3'	101	6.23**
'0' v '4'	50	3.79**
'1' v '2'	84	1.84N.S.
'1' v '3'	98	2.97**
'1' v '4'	47	2.55*
'2' v '3'	112	1.10N.S.
'2' v '4'	61	1.06N.S.
'3' v '4'	75	0.43N.S.

0	1	2	3	4
1.590	2.472	3.140	3.516	3.769

(underlined means not significantly different at 5 per cent level)

[a] Comparisons calculated as for Table 3.20.

of at least two months and the distribution of ovarial development was therefore interesting when compared with that found in newly queenless bees. In the former only 16 per cent of ovaries were found to be inactive and only 6 per cent had fully-developed eggs. The majority were found to have intermediate stages of development - 16 per cent were classified '1', 30 per cent '2' and 32 per cent '3'.

Of interest, too, were sequential changes in the distribution of developed ovaries that took place among the population of newly queenless workers during the first month (mandibular gland analysis page 51). (Table 3.25). Within three days 38 per cent of workers had visibly active ovaries although none had reached stage '2'. After nearly three weeks almost 60 per cent of bees dissected still showed no indication of ovarial activity. The percentage of inactive ovaries eventually diminished; after six weeks only 49 per cent remained inactive, while in the November sample after approximately two months without a queen only 16 per cent were undeveloped.

Five days after queen loss, 8 per cent of the ovaries examined were found to have reached stage '2', and only two days later, 30 per cent of the ovaries assessed were found to be moderately or well developed, 2 per cent of which were found to have fully-developed eggs. The percentage of bees with moderately to well-developed ovaries rose to about 40 per cent after six weeks and to almost 70 per cent

Table 3.25. Sequential changes in ovarial development occurring in A.m.adansonii workers during the first month of queenlessness (February 1979)

Days after queen loss	Percentage distribution of stages of ovarial development				
	0	1	2	3	4
0	100				
3	62	38			
5	60	32	8		
7	59	11	21	7	2
14	51	19	18	7	4
19	58	22	18	2	
38	49	25	*	23	33
80+	16	16	30	32	6

* 38 day sample stages '1' and '3' included stage '2' ovaries
80+ day old bees (November 1979) included for comparison

after two months. The number of bees whose ovaries were fully developed reached the highest level of six per cent after two months of queenlessness. The differences in ovarial activity evident among different age groups are important, not so much at the time they were sampled but rather at the time the queen was removed (Table 3.26). The greatest amount of ovarial activity occurred in the ovaries of bees that were less than three weeks old when the queen was lost. After only three days, 50 per cent of the ovaries of these individuals had begun to develop, the greatest activity being found among ten day olds. Ovarial development in bees that were older than three weeks at dequeening appeared to be retarded in that, although some development did eventually occur, the first active ovaries were found after one week and none was found to have developed beyond stage '2'. Further, ovarial activity in bees that eclosed after loss of the queen also appeared to be slightly retarded. The only five day olds found to have some degree of development were individuals that eclosed two days after dequeening. Those that eclosed later were about ten days old before their ovaries became active.

The only workers, seven in all, that were found to have fully-developed eggs in their ovaries were individuals that had eclosed before the queen was removed but were less than three weeks old at the time. This figure represents a very low percentage as nearly three hundred bees were dissected.

Laying behaviour appeared to be associated with ovarial development as might be expected, however the activity was not limited to individuals with mature eggs. Laying behaviour is here described as the action of inserting the abdomen into cells, and the deposition of eggs is not necessary. Of eight individuals captured while they were inserting their abdomens into cells, two had mature eggs, the others having only moderately to well-developed ovaries (Table 3.27). Six additional workers were seen to be showing laying behaviour, but these escaped capture. These individuals were also under three weeks old at dequeening. Other workers found with mature eggs that were captured during routine sampling were not showing laying behaviour at the time, however it is possible that these individuals could have attained this behaviour.

The only bees that were sampled individually and found to be secreting 9KDA were both less than five days old when the queen was removed from the colony, however neither had mature eggs although their ovaries were well developed.

Table 3.28. Distribution of ovarial development in A. m. adansonii workers of known age in a newly queenless colony (February 1979)

Queenless period before capture (days)	Age at sampling and percentage distribution of stages of ovarial development																								
	5 days					10 days					20 days					30 days					40 days				
	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4	0	1	2	3	4
0	100					100					100					100									
3	55	45				15	85				80	20				100									
5	75	15	10			25	70	5			40	45	15			100									
7	90	10				37	10	27	20	7	68	23	9			53		47							
14	100					47	20	10	23		27	33	33	7		23	27	31	4	15	64	18	18		
19	100					65	15	20			35	25	35	5		30	50	15	5			50	50		

Table 3.27. Ovarial development of queenless A.m. adansonii workers showing laying behaviour (Age in days)

Age at capture/ observation	Age at dequeening	Period queenless	Ovarial development
7	1	7	-
8	1	7	2/3
9	1	8	4/3
13	1	13	3/2
9	2	7	-
10	3	7	3/2
10	3	7	-
16	4	12	3/3
12	5	7	3/2
23	16	77	-
23	16	7	-
28	16	12	2/2
28	17	11	-
32	19	13	4/4

A.m. adansonii worker contact with the queen

Observations relating to worker contact with the queen were made during preparation for the age-related mandibular gland analysis of newly queenless bees (page 51). Courts of worker bees were observed over a period of sixteen days, with a total observation time of about twelve hours. As bees observed attending the queen were not removed, observations of particular individuals could not be regarded as independent and differences could not be tested statistically. In addition, when these observations were made, not all the workers of the colony were marked, and as a result, a number of unmarked individuals were seen attending the queen.

Indications were that the court activities of feeding and licking the queen were performed by two distinct age groups of attendant workers, although there was a considerable overlap (Figure 3.13 and Table 3.28). Those individuals responsible for licking the abdomen of the queen were predominantly older than two weeks, 43.2 per cent being unmarked. It is significant that none younger than six days was seen to lick the queen. In contrast, workers responsible for feeding the queen were predominantly younger than two weeks, only 7.5 per cent were unmarked while 38.8 per cent were less than a week old.

The queen was approximately two months old when these observations

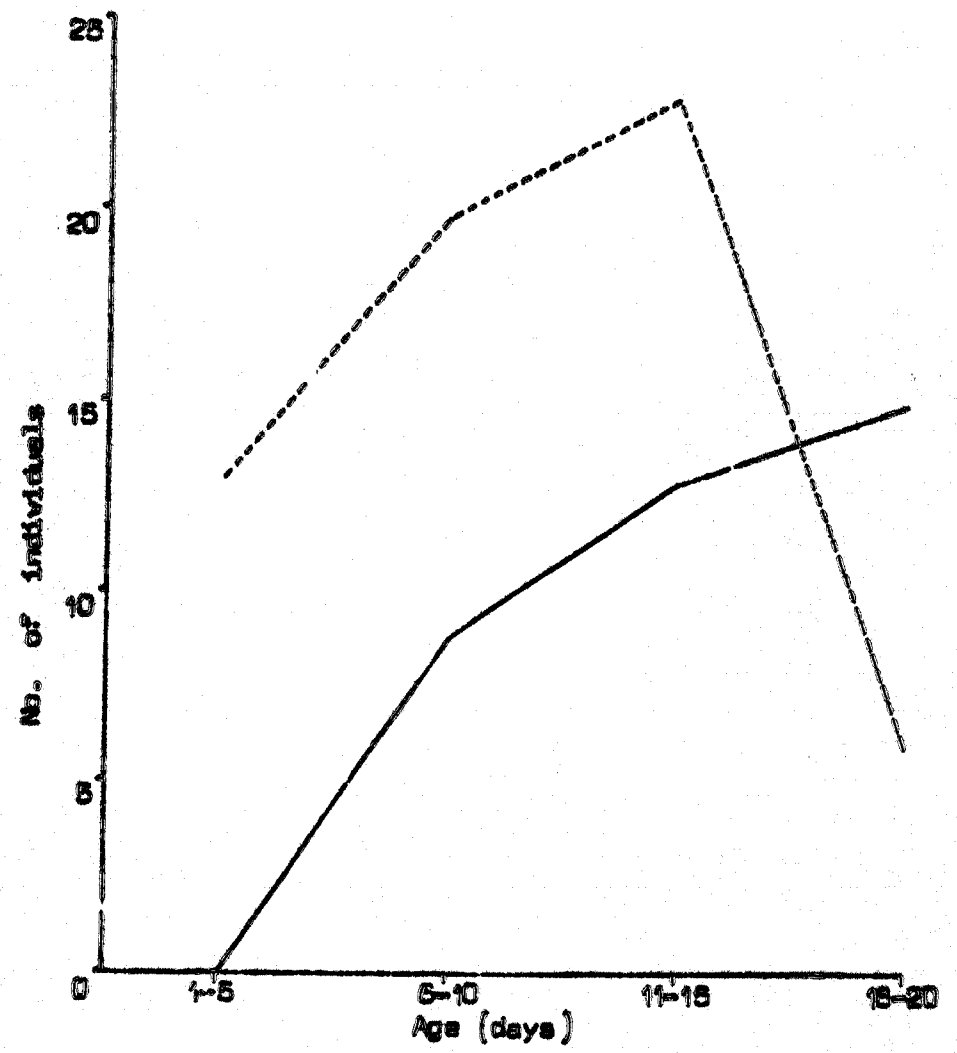


Figure 3.15. Age of workers attendir the queen. —— Bees licking the queen. - - - - Bees feeding the queen

Table 3.28. Ages of workers feeding and licking the queen

Age (days)	Feeding		Licking	
	Count	Percentage	Count	Percentage
1				
2	1			
3	3			
4	3	38.8		2.7
5	6			
6	4		1	
7	9		1	
8	3		3	
9	3		1	
10	1		3	
11	5	38.8	4	28.4
12	4		3	
13	7		4	
14	3		3	
15	4		1	
16			4	
17	3		2	
18		14.9	2	25.7
19	2		4	
20	1		3	
21			3	
Unmarked	5	7.5	32	43.2
Total	67	100.0	74	100.0

were made. She continually attracted an attendant court of over ten workers and occasionally the court numbered as many as twenty. By far the most common behaviour shown by workers in the court was antennal stroking of the queen. Antennal examination was induced almost immediately after a worker met the queen and usually this was the only response. Feeding occurred only sixty seven times in twelve hours, roughly once every ten or eleven minutes, while licking was observed seventy four times, roughly every nine or ten minutes.

These observations suggest that young workers may not be in contact with the same amounts of 9KDA as are their older nestmates, as it is thought that most 9KDA received by workers is licked from the body of the queen during grooming and that very little is received by airborne dispersal (But er, 1954b; S. y 1979).

DISCUSSION

The relevant questions to this discussion are those addressing the relationship between chemical signals, caste differentiation and female intercaste social interactions. In attempting to elucidate these issues the study has provided initial data on the mandibular gland secretions of A.m. adansonii queens and workers in their natural habitat. The investigation has revealed a number of interesting differences that exist between A.m. adansonii and certain other honeybee races including the South African Cape bee, A.m. capensis, and the European bees, A.m. mellifera and A.m. ligustica.

Under normal queenright conditions the A. mellifera queens influence the physiology and behaviour of workers largely by the secretion of 9KDA from the mandibular gland. This influence not only inhibits ovary development in workers and prevents the secretion of 9KDA by their mandibular glands, but probably also regulates normal worker behaviour to a large degree (Reviewed by Gary, 1974; also see Table 1.2). This has become more apparent through recent studies of laying workers that arise during queenless periods. During these periods the influences of the queen are removed, and in A.m. mellifera and more so in A.m. capensis a number of workers undergo extensive ovary development to the point that some have mature eggs in their ovarioles (Perepelova, 1929; Velthuis, 1970b). Simultaneously these individuals cease most normal worker activities and become entirely involved in laying eggs. Not only do these bees change in both their behaviour and their physiology but in addition, their interactions with other workers are affected to a point where they may begin to attract a sizeable court of attendant workers in the same manner as a queen does. These changes in social position are thought to be caused by changes in the mandibular gland signal, as amounts of 9KDA are secreted by laying workers of at least A.m. capensis (Velthuis, 1976; Ruttner, et al, 1976).

Social position among colony members of most socially advanced wasp and bee species (other than spine bees) is established by physical harassment of weaker individuals by stronger ones which results in a distinct dominance hierarchy, the most dominant individuals assuming

the egg-laying role and the subordinates the worker role (Batra, 1966; Cumber, 1949; Free, 1955; Michener, 1974; Michener and Brothers, 1974; Plowright and Jay, 1977; Spradbery, 1973; Wilson, 1971). In Apis mellifera the only display of overt aggression among colony members occurs during the initial periods of queenlessness. Fighting is severe among queenless A.m. capensis workers and hundreds of bees may be killed within a few days. The fighting eventually abates, possibly owing to the establishment of laying workers which may have assumed a dominant position by secreting dominant social signals from the mandibular glands (Anderson, 1963 and 1968).

Morphological differentiation between the queen and worker castes of Apis species and A. mellifera races is advanced and intercastes are almost unknown in natural situations (Eckert, 1934), although they can be produced artificially (Taber and Poole, 1973). Behavioural, physiological and anatomical differentiation, on the other hand, is more variable. While these variations may indicate that caste differentiation within the species and races is merely of a different nature, there is also the possibility that it has evolved to varying degrees. This study has revealed a number of interesting qualities regarding the behavioural, physiological and anatomical differentiation of the female castes of A.m. adansonii which may suggest that caste differentiation and social interaction between queens and workers is markedly different from that found in other A. mellifera races.

In A.m. adansonii, the degree of caste differentiation, which is for all races controlled by nurse workers in the diet fed to developing larvae and which is also almost certainly influenced by the dominant attributes of the queen, is clearly evident in the anatomy of the reproductive system of workers. The mean number of ovarioles per ovary sampled from four populations varied from 2.88 to 4.86 and is consistent with the results of Chaud-Netto and Bueno (1979) although in their study the range was slightly smaller, being one to eleven instead of zero to twelve. With regard to the anatomy of the reproductive system, then, A.m. adansonii workers are similar to A.m. mellifera in that both races have distinctly fewer ovarioles per ovary than any other honeybee yet examined (see Table 4.1).

Velthuis (1976) has suggested that differences between the number of ovarioles in the ovaries of queens and workers is indicative of the degree of difference between the two castes. In this regard, it may be

considered an indicator of the degree of caste differentiation. The immature female at one stage of development has about seventy ovarioles, and it is only differential feeding that causes the number to diminish in one caste and increase in the other (de Wilde, 1976). As A.m.mellifera queens are known to have the largest ovaries; this suggests that caste differentiation is most advanced in A.m. adansonii and A.m. mellifera.

Table 4.1. The number of ovarioles in the ovaries of Apis workers

Species	No. worker ovarioles	
	Mode	Range
Apis dorsata	20	11-53
Apis (indica)=cerana	7	1-30
Apis florea	4	1-9
Apis mellifera capensis	19	5-59
A.m. ligustica	5	1-24
A.m. mellifera	3	1-15
A.m. adansonii	3	0-12

The physiological ability of workers to develop their ovaries during queenless periods can also be regarded as indicative of the degree of differentiation between the female castes. A. (indica)=cerana, A. dorsata and A.m. capensis workers undergo rapid ovarial development and within a few weeks, certain individuals begin laying eggs (Velthuis, 1976). Development among queenless A.m. mellifera and A.m. adansonii workers is relatively slow and this study has shown that in the latter race, functional laying workers do not appear during the first six weeks of queenlessness. The significance of these differences in the ability to undergo ovarial development is associated with behavioural differentiation and should be viewed in that light.

The mandibular gland secretion of queens has for a long time been known to evoke retinue behaviour, suppress ovarial development in workers, and influence a number of other important biological functions (see Table 1.2). Apis dorsata, A. (indica)=cerana and A.m. capensis functional laying workers have been termed false queens as they have been found to evoke marked retinue behaviour and exhibit queen-like behaviour, even to the

extent of suppressing ovarial development in other workers. (Sakagami, 1958, Velthuis, 1976). It is now known that in A.m. capensis, these individuals undergo substantial changes in their mandibular gland signals and begin to secrete significant amounts of 9KDA (Crewe and Velthuis, 1980; Ruttner et al, 1976). Recently, it has been found that the functional laying workers of A.m. mellifera also secrete appreciable amounts of 9KDA, supporting observations that these individuals are capable of evoking retinue behaviour and inhibiting ovarial development in others, although to a lesser degree than the false queens of A.m. capensis (Crewe and Velthuis, 1980; Velthuis et al, 1965).

In contrast, A.m. adansonii laying workers have never been observed to evoke retinue behaviour, and this study has shown that very few individuals are capable of secreting 9KDA. As was predicted by Velthuis (1976) for A.m. mellifera, many A.m. adansonii workers experienced some degree of ovarial activity. The number of 'indifferent' bees (a term Velthuis used to describe individuals whose ovaries remain inactive), remained at between 50 and 60 per cent during the first five weeks of queenlessness, while in a separate investigation they were found to number only 16 per cent after two months without a queen. Very few bees (less than 3 per cent of those that had been queenless less than six weeks, and only 6 per cent of those queenless for at least two months) were found to have mature eggs in their ovaries. While it is necessary to take into account environmental influences (that is, influences of season, quantities of available food, numbers of nurse bees and condition of the queen) the substantial difference in ovarial development between these two queenless groups is probably due largely to the length of time the bees had been without a queen. With time, more and more bees were able to develop their ovaries, the great majority to stages '2' and '3', an important difference between A.m. adansonii and other races in which laying workers begin to suppress ovarial development in time.

During the investigation of newly-queenless bees, only fourteen were observed inserting their abdomen into cells although none laid eggs (Table 3.23). Of these, eight were captured and what is significant is that only two had mature eggs and neither was secreting 9KDA. Only one individual was found to be secreting 9KDA and this bee merely had well-developed ovaries (degree '3') but did not have mature eggs. The remaining five had neither mature eggs in their ovaries nor 9KDA in their mandibular gland secretion. Ovarial activity, glandular activity and queenlike behaviour must however be loosely allied, since the secretion of 9KDA

and egg-laying behaviour were always associated with at least well-developed ovaries (degree '3').

Regarding social interaction, caste differentiation and the dominance of the queen, one of the most important aspects of A.m. scutellonii biology to emerge clearly is that workers appear to be incapable of secreting sufficient quantities of 9KDA. This despite the fact that the two individuals found to have 9KDA in their mandibular glands were secreting larger amounts of the chemical than were A.m. capensis and A.m. mellifera laying workers (Crewe and Velthuis, 1980). None of the bees observed attracted courts of any size and overt aggression was limited to mild harassment such as wing and leg holding and occasional attempts to sting. The only indications that some influence may have been exerted by either specific individuals or by the queenless colony as a whole, was the fact that bees emerging after the colony had lost the queen appeared to be retarded in their ability to develop their ovaries.

The most active workers were those that had emerged at the time the queen was lost but which were then younger than three weeks. All individuals found to have mature eggs, as well as all those that showed laying behaviour were from this group. In addition, the two individuals found to be secreting 9KDA were less than a week old when the colony became queenless.

Bees older than three weeks at the time the queen was removed were also retarded in their ability to undergo ovarial development. Whereas up to 85 per cent of ten day olds had experienced some development within three days, three week old bees took up to a week before their ovaries became active.

It appears that two separate factors are responsible for these differences between the different age groups of workers, namely the influences of the queen prior to her loss and the influences of queenless workers following her loss, the former being considerably more powerful. Figure 3.15 indicated that very young bees are primarily responsible for feeding the queen and that it is the older ones that lick the queen. With regard to the hypothesis of the mechanism of 9KDA transport by workers proposed by Butler (1954b), namely that workers lick the substance off queens and transmit it to other colony members trophollactically, these observations of an age-related difference in retinue behaviour by worker bees are provocative. The observations suggest that the exposure of very young

and egg-laying behaviour were always associated with at least well-developed ovaries (degree '3').

Regarding social interaction, caste differentiation and the dominance of the queen, one of the most important aspects of A.m. adansonii biology to emerge clearly is that workers appear to be incapable of secreting sufficient quantities of 9KDA. This despite the fact that the two individuals found to have 9KDA in their mandibular glands were secreting larger amounts of the chemical than were A.m. capensis and A.m. mellifera laying workers (Crewe and Velthuis, 1980). None of the bees observed attracted courts of any size and overt aggression was limited to mild harassment such as wing and leg holding and occasional attempts to sting. The only indications that some influence may have been exerted by either specific individuals or by the queenless colony as a whole, was the fact that bees emerging after the colony had lost the queen appeared to be retarded in their ability to develop their ovaries.

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bees to 9KDA is minimal, being limited to antennal contact with the queen and to trophallaxis, while older individuals are subject to greater amounts owing to their licking the queen. If this is true, and the effects of 9KDA are accumulative, and provided that the chemical is systemic rather than olfactory in its action, then the influences of 9KDA upon the physiology and behaviour of workers are likely to be more reversibly in young bees than they are in older individuals, and therefore after loss of the queen, it would be the younger bees that would rapidly undergo physiological and behavioural change, while their older nestmates would require a longer period before the influences of the queen's signals dissipate. However, recently Seeley (1979) was unable to extract more than one nanogram of 9KDA from bees that left the retinue, thereby seriously questioning the reasoning of this argument. He found that the dispersion of 9KDA was largely carried out by 'messenger' bees leaving the retinue and dispersing the queenright message through olfaction, supporting the surface transport hypothesis of Verheijen-Voogd (1959). The differences regarding the ability of workers of various ages to develop their ovaries at the onset of queenlessness is more likely, then, to be a simple consequence of aging and have no connection with exposure to 9KDA at all.

Workers that emerge in queenless colonies, emerge into a situation in which the influence of the queen has been replaced by the influence of queenless workers.

Among queenless A.m. adansonii colonies this influence may be due to the combined amount of 9KDA secreted by a number of individuals. In the newly queenless colony investigated in this study, a total amount of 378,3 micrograms of 9KDA was detected from twelve samples. While this amount compares favourably with the amounts secreted by individual queens, it did no more than retard ovarial development in newly-emerged bees. It is clear that despite the level of 9KDA being as high as that of a normal queenright colony, additional factors that allow recognition of the queen have possibly not been simulated in the queenless situation in A.m. adansonii. It is possible that the high level of 9KDA is not sustained. However an alternative explanation is that as 9KDA-secreting individuals are not apparently recognised as such by other workers, distribution of the compound is not adequate enough to induce a queenright situation, although it is sufficient to retard ovarial development in bees that subsequently eclose into the queenless situation.

The study revealed that the majority of workers do not experience marked changes in their mandibular gland secretion despite undergoing considerable ovarial development. It is not unreasonable to suggest that caste differentiation in a hypothetical Apis race could be complete enough to prevent workers from changing the secretion of the mandibular gland. Just as morphological and anatomical attributes are narrowly determined, so it is possible to argue that physiological and behavioural attributes may also be canalised. The degree to which these features are capable of change would indicate the level of caste differentiation experienced by individuals during their development.

A.m. adansonii workers, on the whole, do not experience marked changes in the mandibular gland secretion during queenless periods, however changes that do occur appear to be toward a queenlike secretion. No trace of 9KDA was found in over 99 per cent of queenless bees analysed, and substantial amounts were found in only two individuals. The mandibular gland secretions of these workers were almost identical to those of queens except that the quantities of most components were greatly reduced. The fact that they failed to elicit court behaviour among surrounding nestmates suggests that their signals, though qualitatively similar to queen signals, were quantitatively inadequate.

The displays of overt aggression that occur in queenless colonies of A.m. mellifera are not between laying workers but instead the laying workers are attacked by aggressive nestmates with moderately developed ovaries (Velthuis, 1976). The layers appear to be submissive toward their aggressors and never attempt to defend themselves but only attempt to escape. Velthuis equates these aggressive reactions with behavioural dominance and raises the question of laying workers being reproductively dominant yet behaviourally submissive. An alternative explanation could be that these laying workers are behaving in a manner similar to strange, introduced queens who offer no resistance when confronted by aggressive workers and may even be killed if unable to escape. Szabo (1974a) found that if strange queens were either less attractive or more attractive to workers than was their own queen, workers behaved aggressively towards them. However, queens that had similar degrees of attraction were accepted without any aggressive reactions. In A.m. mellifera, laying workers possibly secrete queenlike signals in sufficient strength to be regarded as strange queens thereby eliciting aggressive tendencies in nestmates, and their inability to reciprocate aggressively may be due to queenlike behaviour. Rather than being regarded as submissive, then, they should

be regarded as behaviourally different.

The lack of overt aggression in queenless A.m. adansonii colonies, in the light of the above argument, may be due to the fact that laying workers are incapable of secreting queenlike signals in sufficient amounts to reach a level necessary to evoke aggressive reactions in nestmates. While it is possible that the level is higher for A.m. adansonii than for A.m. mellifera, the evidence suggests that it is more likely that A.m. adansonii workers have a very limited ability of secreting 9KDA despite being able to develop their ovaries. In other words, A.m. adansonii laying workers are incapable of functioning as false queens.

The object of making colonies queenless is in fact simply to induce a single caste situation in which a pseudo caste differentiation can develop based purely upon physiological and behavioural changes among equal nestmates. It follows that the queen suppresses these expressions in queenright situations and that the degree to which these expressions are present in the worker caste depends upon the degree to which the caste has differentiated. The more complete this differentiation is, the more queenlike and the more workerlike the two female castes are and the more unlikely it is that pseudo differentiation will occur in the absence of the influences of the queen.

> 'With increasing polymorphism the potencies of the two female castes become more distinct. In fact, in the orphan colony the workers are brought back in an antique situation in the evolution of their species : the females are all more or less alike. What they do in this situation depends on what remains of their antique equipment, thus pointing to the origin from which both queen and worker are derived'. Velthuis, 1976.

The antique equipment referred to in this quotation must include all the attributes, both morphological, anatomical, physiological and behavioural, which normal ancestral females would possess. Following caste differentiation most of the attributes regarding dominance and reproduction are irreversibly lost from the worker caste, and those that remain are suppressed by the communication of dominant signals by the queen individual. From the evidence provided in this study, and in the light of the above argument, it would appear that caste differentiation in A.m. adansonii is at a level high enough to render the worker caste unable to secrete dominant mandibular gland signals, despite certain individuals being able to alter their signals to some extent.

The suppressive ability of the queen is almost certainly associated

with her mandibular gland signal. The average secretion of mated A. m. adansonii queens was found to have very significant differences in the amounts and proportions of certain components compared to that of A. m. mellifera queens (Callow et al, 1964). The average amount of 9KDA was 250.5 micrograms (Table 3.1) compared with their two hundred micrograms. The level of 9HDA was lower, averaging only 80.9 micrograms (Table 3.1) compared with one hundred and fourteen micrograms in A. m. mellifera queens. Consequently these important queen pheromones were found in a very different ratio in A. m. adansonii queens. While the 9KDA : 9HDA ratio in A. m. mellifera queens was nearly 10:6 (Simpson, 1979), in the queens of A. m. adansonii the ratio was only 10:3. Recently Crewe and Velthius (1980) found that in five mated, laying A. m. mellifera queens the 9KDA : 9HDA ratio was nearly 10:9. The queens produced on average 71.2 micrograms of 9KDA and 63.5 micrograms of 9HDA, the chemicals constituting 36.1 per cent and 32.2 per cent of the acid secretion respectively.

Of additional interest were the levels of DAA, a compound that is not known to have specific biological activity. While the amounts of DAA are reasonably high in A. m. mellifera queens (twenty five microgram per head)(Simpson,1979), the amounts were extremely low in the queens of A. m. adansonii, averaging only 2.4 micrograms (Table 3.1). Consequently the 9KDA : DAA ratios were very different, being 8:1 in the former race and 100:1 in the latter. In contradiction, Crewe and Velthuis (1980) found no trace of DAA in A. m. mellifera queens during their recent study. The level of DAA in A. m. mellifera workers has not induced comment in the literature, and it can only be concluded then that the compound is probably not found in appreciable quantities in these individuals. In contrast, DAA was usually found to be a major component of the mandibular gland secretion of older A. m. adansonii workers. While the levels of DAA in A. m. mellifera queens and workers appear to arouse little interest, the levels found in the female castes of A.m. adansonii do. In younger workers DAA was found to be consistently less than 5 per cent of the secretion, but after the first week of life bees began to increase their secretion of DAA until the compound regularly comprised over 25 per cent of the secretion, and in one bee surpassed 50 per cent (Appendix Table 6). The biological function of DAA, if any, is unknown, however in queenless bees the amount of DAA decreased considerably with ovarial development, and in individuals

with well developed ovaries was absent, suggesting that the compound may in some way be a consequence of worker suppression in A.m. adansonii.

Levels of 2-heptanone, an alarm pheromone secreted by the mandibular glands of worker honeybees (Maschwitz, 1964) were also found to decrease substantially with ovarial development. In the only group of queenless bees analysed for 2-heptanone, the average amount was found to decrease from 17.9 micrograms per head in workers with undeveloped ovaries to 0.4 micrograms per head in workers whose ovaries contained mature eggs (Figure 3.10,Table 3.15). The decreased level of 2-heptanone in queenless colonies may well influence the behaviour of such a group, and it is possible that this feature is a contributing factor to queenless bees often being noticeably less aggressive towards intruders than their queenright counterparts (personal observation)

Velthuis (1976) concluded that for 'Apis the capacity of the worker to develop into a false queen is limited'. The degree to which workers are capable of becoming false queens in various species and races of Apis depends upon the degree of caste differentiation, a process that is almost certianly influenced by the mandibular gland signals of the queen. This study has revealed that the queens of A.m. adansonii have a markedly different mandibular gland signal from A.m. mellifera queens, mated, laying individuals secreting considerably greater amounts of most of the acids including 9KDA,9HDA and 10HDA, and having a markedly different 9KDA:9HDA ratio than their european counterparts. In addition it has shown the amounts of 10HDA in queenright workers are reasonably similar to those found in European workers (Boch and Shearer, 1967) although the chemical appeared to be more prevalent in younger bees, two to five day olds having an average of 43.1 micrograms, and six to eighteen hour olds having 13.9 micrograms. It is possible that this early secretion of 10HDA represented an accumulation of the chemical prior to the onset of nursing behaviour, 10HDA being the main lipoid component of larval food (Barker et al,1959), as the chemical decreased noticeably in seven to ten day olds. Although it later increased to an average of 47.8 micrograms in fifteen day olds, it subsequently declined to only 19.9 micrograms in four week old bees. The study has also shown that the total absence of false queens in queenless groups of this race is not the result of an inability to develop the ovaries (functional laying workers are present in all queenless A.m. adansonii colonies) but rather the result of an inability to alter adequately the mandibular gland worker signal to a queenlike signal. While this is so, certain

significant changes in the biology of queenless bees did occur, suggesting a shift toward queenness. There was a substantial increase in longevity, queenless bees living at least twice as long a queenright individuals. Numerous workers experienced ovarial development and a few began to lay eggs. Workers with developed ovaries had decreased levels of DAA and 2-heptanone, both features of the mandibular gland secretion of the queen, and a small percentage began to secrete 9KDA.

Initially, queenless workers were also found to undergo a rapid and substantial decrease in the secretion of 10HDA, levels dropping from an average of 33.6 micrograms in ten samples just prior to dequeening to only 7.9 micrograms in thirty six samples during the first two weeks of queenlessness. The cause of this drop is unknown and no reasonable explanation is apparent as larvae were not present in the colony. With time workers began to secrete more 10HDA and in bees that had been queenless for over two months the average secretion contained 32.1 micrograms of 10HDA. Another interesting feature was the differences in the secretion of 10HDAA and especially 10HDA in these workers, the levels of these chemicals increasing significantly with ovarial development (Figure 3.11). The increase in the amount of 10HDA very closely followed a decrease in 2-heptanone, which, in view of the opinion of Simpson (1960), may further suggest that 2-heptanone is derived from the breakdown of 10HDA.

Despite the initial changes toward queenlike signals in the mandibular gland secretions of newly queenless bees, including the secretion of 9KDA, no workers evoked retinue behaviour among nestmates and ovarial development was not inhibited. In addition, overt aggressive reactions in newly queenless colonies were minor and no individuals were stung to death.

Although these data were compiled from observations of only a few colonies, and generalisations must therefore be viewed cautiously, together they indicate that the relationships between the queen and worker castes in A.m. adansonii may possible be more advanced than in most races. They suggest that the process of caste differentiation may be so complete, morphologically, anatomically and physiologically as to exclude all workers from altering their behavioural position sufficiently to imitate the queen, explaining why 'false' queens have never been observed in queenless colonies despite the presence of laying workers. It was hoped that data gathered from the small cage study would provide evidence of the extent to which A.m. adansonii

workers were capable of dominating other individuals during queenless periods, however the experiment was inconclusive due to an alimentary ailment which interfered with normal behaviour and caused the premature death of a number of individuals. At that stage, the ovaries of all bees had just become active (although none had begun to decompartmentalise) and although three individuals were found to have minute amounts of 9KDA in their mandibular gland secretion, in general, secretions were not significantly different in their composition.

Some of the most interesting features emerging from this study, then, were the apparent secretion of mature mated queen signals by A.m.pdansonii queens in which at least the 9KDA:9HDA:10HDA ratio is reasonable homogenous ; the significance of the age of workers at the time the queen is lost on their ability to undergo changes toward a queenlike disposition while queenless ; the discovery that these changes (the secretion of queenlike mandibular gland signals, ovarial development and laying behaviour) are not necessarily synchronous ; and lastly, the unexpected prominence of DAA in the mandibular gland secretions of older workers.

The study showed conclusively that the mandibular gland secretions of virgin queens are very dissimilar from those of mated queens, especially during the first two to three days of life. Also the dissimilarity between the secretions of different virgins indicated that their mandibular glands were probably in a transitory phase of activity. The sample size was, however, too small to reveal the precise timing and sequence of these changes.

The possibility of there being a mature mated queen signal (in this study the 9KDA:9HDA:10HDA ratio was approximately 10:4:2 and the three components composed 80 per cent of the acid secretion) raised some interesting questions. Is the signal age related, in other words, do all queens achieve a mature signal at some stage? Is the signal related to the season or to intrahival conditions? Is it related to the development period of the individual and to weight; in other words are some queens unable to achieve a mature signal? And most importantly, if certain queens do not achieve the signal (as appears to be the case from this study) can this inability be related to factors in the colonies they head; factors such as small colony size, poor brood patterns and perhaps a poor foraging behaviour?

The study very definitely showed that workers that experience the most rapid and most complete changes in their anatomy, physiology and behaviour, are those that eclosed from a week after queen loss to two weeks before queen loss. The relationships between changes in the mandibular gland secretion, ovarial development and laying behaviour that occur in these individuals were not clear, although this study did show that the changes appeared to be neither consecutive nor synchronous in their occurrence. Of interest was the marked drop in the level of 2-heptanone that occurred in the mandibular gland secretion of workers experiencing ovarial development. The phenomenon raises the question of what happens to the secretions of other honeybee glands, and in particular, what happens to iso-pentyl acetate in the sting gland?

Lastly, the study unexpectedly revealed DAA as a major component in the mandibular gland secretions of A.m. adansonii workers. This chemical, which has never evoked comment in apicultural literature, was found to increase markedly with age, and in certain three to four week old bees became the most abundant component of the secretion. It's production was found to decrease rapidly with ovarial development, and in bees with well-developed ovaries DAA was a minor component, correlating with the situation found in queens. It's prominence in workers and its insignificance in queens, together with its sharp decline in workers experiencing ovarial development, suggests that this chemical is somehow associated with queenness and may even have an as yet unknown biological function in A.m. adansonii.

It is hoped that this study will initiate added interest in A.m. adansonii and induce further research into some of the questions raised during the discussion.

BIBLIOGRAPHY

Alexander, R.D. 'The evolution of social behaviour'. Ann. Rev. Ecol. Syst., 5 : 325-383, 1974.

Anderson, R.D. 'The laying worker of the Cape honeybee, Apis mellifera capensis'. J. apicult. Res., 2(2) : 85-92, 1963.

———. 'The effect of queen loss on colonies of Apis mellifera capensis'. S. Afr. J. agric. Sci., 11(2) : 383-387, 1968.

———. 'Some Aspects of the biology of the Cape honeybee'. In African Bees : Taxonomy, Biology and Economic Use, ed. D.J.C. Fletcher. Apimondia International Symposium, Pretoria, pp 107-114, 1977.

———, Buys, S., Johannsmeier, M.F. 'Beekeeping in South Africa'. S. Afr. Dep. Agric. Tech. Serv., Bulletin No. 394, 191pp, 1973.

Asencot, M., Lensky, Y. 'The effects of sugars and juvenile hormone on the differentiation of the female honeybee larvae (Apis mellifera L.) to queens'. Life Sci., 18(7) : 693-700, 1976.

———, Lensky, Y. 'The effect of sugar crystals in stored royal jelly and juvenile hormone on the differentiation of female honeybee (Apis mellifera L.) larvae to queens'. Suppl. Proc. VIIIth Int. Congr. I.U.S.S.I., Wageningen, The Netherlands, 1977.

Barbier, M., Lederer, E. 'Structure chimique de la "substance royale" de la reine d'abeille (Apis mellifera L.)'. C. R. Acad. Sci. Paris (D)., 250(26) : 4467-4469, 1960.

———, Lederer, E., Namura, T. 'Synthese de l'acide cis-9 decene-2-trans oique ("substance royale") et de l'acide cis-8 nonene-2-trans oique'. C. R. Acad. Sci. Paris (D)., 251(10) : 1133-1135, 1960.

Barker, S.A., Foster, A.B., Lamb, D.C., Jackman, L.M. 'Biological origin and configuration of 10-hydroxy-Δ2-decenoic acid'. Nature, Lond., 184 : 634, 1959.

Batra, S.W.T. 'Life cycle and behaviour of the primitively social bee, Lasioglossum zephyrum'. Univ. Kansas, Sci. Bulletin No. 46 : 359-423, 1966.

Beetsma, J. 'The process of queen-worker differentiation in the honeybee'. Bee World, 60(1) : 24-39, 1979.

Bertholf, L.M. 'The moults of the honeybee'. J. econ. Ent., 18(2) : 380-384, 1925.

Blum, M.S., Boch, R., Doolittle, R.E., Tribble, M.T., Traynham, J.G. 'Honeybee sex attractant : conformational analysis, structural specificity, and lack of masking activity of congeners'. J. Insect Physiol., 17(2) : 349- 364, 1971.

———, Fales, H.M., Tucker, K.W., Collins, A.M. 'Chemistry of the sting apparatus of the worker honeybee'. J. apicult. Res., 17(4) : 218-221, 1978.

Boch, R., Shearer, D.A. 'Identification of geranial as the active component in the Nasonoff pheromone of the honey bee'. Nature Lond., 194 : 704-706, 1962.

———, Shearer, D.A. '2-heptanone and 10-hydroxy-trans-dec-2-enoic acid in the mandibular glands of worker honey bees of different ages'. Z. vergl. Physiol., 54 : 1-11, 1967.

———, Shearer, D.A., Petrunovits, A. 'Efficacies of two alarm substances of the honey bee'. J. Insect Physiol., 16(1) : 17-24, 1970.

———, Shearer, D.A., Stone, B.C. 'Identification of iso-amyl acetate as an active component in the sting pheromone of the honey bee'. Nature, Lond., 195 : 1018-1020, 1962.

Butler, C.G. ' 'The World of the Honeybee'. (New Naturalist Series). Collins, London, 1954a.

———. 'The method and importance of the recognition by a colony of honeybees (A. mellifera) of the presence of its queen'. Trans. R. ent. Soc. Lond., 105(2) : 11-29, 1954b.

———. 'Mandibular gland pheromone of worker honeybees'. Nature, Lond., 212 : 530, 1966.

———. 'The queen and the "spirit of the hive"'. Proc. R. ent. Soc. Lond.(C)., 37 : 59-65, 1973.

———, Calam, D.H. 'Pheromones of the honey bee - the secretion of the Nasonoff gland of the worker'. J. Insect Physiol., 15(2) : 237-244, 1969.

———, Callow, R.K. 'Pheromones of the honeybee (Apis mellifera L.) : the "inhibitory scent" of the queen'. Proc. R. ent. Soc. Lond. (B)., 43 : 62-65, 1968.

———, Fairey, E.M. 'The role of the queen in preventing oogenesis in worker honeybees'. J. apicult. Res., 2(1) : 14-18, 1963.

———, Fairey, E.M. 'Pheromones of the honeybee : biological studies of the mandibular gland secretion of the queen'. J. apicult. Res., 3(2) : 63-76, 1964.

———, Gibbons, D.A. 'The inhibition of queen rearing by feeding queenless worker honeybees (A. mellifera) with an extract of "queen substance"'. J. Insect Physiol., 2 : 51-54, 1958.

———, Paton, P.N. 'Inhibition of queen rearing by queen honey-bees (Apis mellifera L.) of different ages'. Proc. R. ent. Soc. Lond. (A)., 37(7-9) : 114-116, 1962.

———, Simpson, J. 'The source of the queen substance of the honey bee (Apis mellifera L.)'. Proc. R. ent. Soc. Lond. (A)., 33(7-9) : 120-122, 1958.

———, Simpson, J. 'Pheromones of the honeybee (Apis mellifera L.) : An olfactory pheromone from the Koschewnikow's gland of the queen'. Vedecke Prace Vyzkumnych Ustavu Zemedelskych Vcelarskych v Dole, pp. 33-36, 1965.

———, Simpson J. 'Pheromones of the queen honeybee (Apis mellifera L.) whir enable her workers to follow her when swarming'. Proc. R. ent. Soc. Lond. (A)., 42(10-12) : 149-154, 1967.

———, Callow, R.K., Chapman, J.R. '9-hydroxydec-trans-2-enoic acid, a pheromone stabilizing honeybee swarms'. Nature,Lond., 201 : 733, 1964.

———, Callow, R.K., Johnston, N.C. 'The isolation and synthesis of queen substance, 9-oxodec-trans-2-enoic acid, a honeybee pheromone'. Proc. R. Soc. (B)., 155 : 417-432, 1962.

———, Fletcher, D.J.C., Watler, D. 'Nest-entrance marking with pheromones by the honeybee Apis mellifera L., and by a wasp, Vespula vulgaris L.'. Anim. Behav., 17 : 142-147, 1969.

———, Fletcher, D.J.C., Watler, D. 'Hive entrance finding by honey bee (Apis mellifera L.) foragers'. Anim. Behav., 18 : 78-91, 1970.

———, Callow, R.K., Koster, C.G., Simpson, J. 'Perception of the queen by workers in the honeybee colony'. J. apicult. Res., 12(3) : 159-166, 1973.

Callow, R.K., Johnston, N.C. 'The chemical constitution and synthesis of queen substance of honeybees (Apis mellifera)'. Bee World, 41(6) : 152-153, 1960.

———, Chapman, J.R., Paton, P.N. 'Pheromones of the honeybee : chemical studies of the mandibular gland secretion of the queen'. J. apicult. Res., 3(2) : 77-89, 1964.

Chai, Ber-Lin, Shuel, R.W. 'Effects of supernumerary corpora allata and farnesol compounds on ovary development in the worker honeybee'. J. apicult. Res., 9(1) : 19-27, 1970.

Chaud-Netto, J., Bueno, O.C. 'Number of ovarioles in workers of Apis mellifera adansonii and Apis mellifera ligustica : A comparative study'. J. apicult. Res., 18(4) : 260-263, 1979.

Chauvin, R. 'Sur l'epagine e et sur les glandes tergales d'Arnhart'. Insectes Soc., 9 : 1-5, 1962.

Copijn, G.M., Beetsma, J., Wirtz, P. 'Queen differentiation and mortality after application of different juvenile hormone analogues to worker larvae of the honeybee (Apis mellifera L.)'. Proc. K. ned. Akad. Wet. (C)., 82(1) : 29-42, 1979.

Crewe, R.M., Hastings, H. 'Production of pheromones by workers of Apis mellifera adansonii'. J. apicult. Res., 15(3/4) : 149-154, 1976.

_____, Velthuis, H.H.W. 'False queens: A consequence of mandibular gland signals in worker honeybees'. Naturwissenschaften, 67: 467-469, 1980.

Cumber, R.A. 'The biology of humble-bees, with special reference to the production of the worker caste'. Trans. R. ent. Soc. Lond., 100(1) : 1-45, 1949.

Dietz, A., Lambremont, E.N. 'Caste determination in honeybees. II. Food consumption of individual honey bee larvae, determined with ^{32}P-labelled royal jelly'. Ann. ent. Soc. Am., 63(5):1342-1345, 1970.

Doueult, P., Roger, B., Pain, J. 'Mise en evidence, au moyen d'un radio-isotope, d'une variation saisonniere dans les transferts de nourriture entre ouvrieres d'abeilles (Apis mellifera ligustica S.)'. C. R. Acad. Sci. Paris (D)., 275:2399-2402,1975.

Eckert, J.E. 'Studies in the number of ovaries in queen honeybees in relation to body size'. J. econ. Ent., 27(3):629-635, 1934.

Free, J.B. 'The behaviour of egg-laying workers of bumblebee colonies'. Br. J. Anim. Behav., 3 : 147-153, 1955.

_____. 'The transmission of food between worker honeybees'. Br. J. Anim. Behav., 5(2) : 41-47, 1957.

_____. 'The transfer of food between the adult members of a honeybee community'. Bee World, 40(8) : 193-201, 1959.

_____, Butler, C.G. 'Bumblebees'. (New Naturalist Series)., Collins, London, 1959.

Gary, N.E. 'Queen honeybee attractiveness as related to mandibular gland secretion'. Science, N.Y., 133 : 1479-1480, 1961a.

_____. 'Antagonistic reactions of worker honeybees to the mandibular gland contents of the queen'. Bee World, 42 : 14-17, 1961b.

_____. 'Chemical mating attractant in the queen honey bee'. Science, N.Y., 136 : 773-774, 1962.

_____. 'Observations of mating behaviour in the honey bee'. J. apicult. Res., 2(1) : 3-13, 1963.

_____. 'Pheromones that affect the behaviour and physiology of honeybees'. In Pheromones, ed. M.C. Birch. Amsterdam, Netherlands, 1974.

_____, Morse, R.A. 'Queen cell construction in honey bee (Apis mellifera L.) colonies headed by queens without mandibular glands'. Proc. R. ent. Soc. Lond. (A)., 37 (7-9) : 76-78, 1962.

Gehrke, C.W., Leimer, K. 'Trimethylsilylation of Amino acids : derivatization and Chromatography'. J. Chromat., 57 : 219-238, 1971.

Goewie, E.A. 'Regulation of caste differentiation in the honey bee (Apis mellifera L.)'. Agricultural University, Wageningen : Thesis 78(15), 1978.

————, Beetsma, J. 'Induction of caste differentiation in the honey bee (Apis mellifera L.) after topical application of JH-III'. Proc. K. ned. Akad. Wet. (C)., 79(5) : 466-469, 1976

Hagenguth, H., Rembold, H. 'Identification of juvenile hormone 3 as the only JH homolog in all developmental stages of the honey bee'. Z. Naturf. (C) 33(11-12) : 847-850,1979.

Hamilton, W.D. 'The genetical evolution of social behaviour, I and II'. J. theor. Biol., 7 : 1-16, 17-52, 1964.

————. 'Altruism and related phenomena, mainly in social insects'. Ann. Rev. Ecol. Syst., 3 : 193-232, 1972.

Haydak, M.H. 'Larval food and development of castes in the honeybee'. J. econ. Ent., 36(5) : 778-792, 1943.

Hess, G. 'Uber den Einfluss der Weisellosigkeit und des Fruchtbarkeits vitamins E auf Ovarien der Bienenarbeiterin'. Beih. schweiz. Bienenztg., 1(2) : 33-110. 1942.

Jay, S.C. 'Factors influencing ovary development of worker honeybees under natural conditions'. Can. J. Zool., 46(3) : 345-347, 1968.

————. 'The effect of various combinations of immature queen and worker bees on the ovary development of worker honeybees in colonies with and without queens'. Can. J. Zool., 48(1) :169-173, 1970.

————. Ovary development of worker honeybees when separated from worker brood by various methods'. Can. J. Zool., 50(5) : 661-664, 1972.

————. 'Factors influencing ovary development of worker honeybees of European and African origin'. J. Can. Zool., 53(10):1387-1390,1975.

————, Jay, D.M. 'The effect of various types of brood comb on the ovary development of worker honeybees'. Can. J. Zool., 54(10) : 1724-1726, 1976.

————, Nelson, E.V. 'The effects of laying worker honeybees (Apis mellifera L.) and their brood on the ovary development of other worker honeybees'. Can J. Zool., 51(6) : 629-632, 1973.

Jaycox, E.R. 'Honeybee queen pheromones and worker foraging behaviour'. Ann. ent. Soc. Am., 63(1) : 222-228, 1970.

Jung-Hoffman, I. 'Die Determination von Konigin und Arbeiterin der Honigbiene'. Z. Bienenforsch., 8 : 296-322, 1967.

Kneer, G., Atwood, C.E. 'Polymorphism in some nearctic halictine bees'. Science, N.Y. 152 : 1262-1263, 1966.

Koeniger, N., Weiss, J. Maschwitz, U. 'Alarm pheromones of the sting in the genus Apis'. J. Insect Physiol., 25(6) : 467-476, 1979.

Kropacova, S., Haslbachova, H. '. The development of ovaries in worker honeybees in a queenright colony'. J. apicult. Res., 8(2) : 57-64, 1969.

————, Haslbachova, H. 'The development of ovaries in worker honeybees in queenright colonies examined before and after swarming'. J. apicult. Res., 9(2) : 65-70, 1970.

————, Haslbachova, H. 'The influence of queenlessness and of unsealed brood on the development of ovaries in worker honeybees'. J. apicult. Res., 10(2) : 57-61, 1971.

Levin, M.D., Haydak, M.H. 'Seasonal variation in weight and ovarian development in the worker honeybee'. J. econ. Ent., 44(1) : 54-57, 1951.

Lin, N., Michener, C.D. 'Evolution of sociality in insects'. Q. Rev. Biol., 47(2) : 131-159, 1972.

Maschwitz, U.W. 'Alarm substances and alarm behaviour in social Hymenoptera'. Nature, Lond., 204 : 324-327, 1964.

Malempy, R.M. Willis, E.R. 'Respiratory metabolism during larval and pupal development of the female honeybee (Apis mellifera L.)'. Physiol. Zoöl., 12(3) : 302-311, 1939.

Michener, C.D. 'Comparative social behaviour of bees'. Ann. Rev. Ent., 14 : 299-342, 1969.

————. 'The Social behaviour of bees : a comparative Study'. Belknap Press, Harvard Univ. Press, Camb, Mass., 1974.

————, Brothers, D.J. 'Were workers of eusocial Hymenoptera initially altruistic or oppressed?'. Proc. Nat. Acad. Sci. USA., 71(3) : 671-674, 1974.

Morse, R.A. 'Honeybee alarm pheromone : another function'. Ann. ent. Soc. Am., 65(6) : 1430, 1972.

————, Boch, R. ' Pheromone concert in swarming honey bees. (Hymenoptera : Apidae)'. Ann. ent. Soc. Am., 64(6) : 1414-1417, 1971.

Osanai, M., Rembold, H. 'Entwicklungsabhangige mitochondriale Enzymaktivitäten bei den Kasten der Honigbiene'. Biochim. biophys. Acta, 162 : 22-31, 1968.

Pain, J., Roger, B. 'Variation annuelle de l'acide hydroxy-10 decene - 2 oique dans les tetes d'abeilles'. Apidologie, 1(1) : 29-54, 1970

————, Roger, B. 'Rythme circadien des acides ceto-9 decene-2 oique, pheromone de la reine, et hydroxy-10 decene-2 oique des ouvrieres d'abeilles Apis mellifera ligustica'. Apidologie, 9(4) : 263-272, 1978.

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