INFLUENCE OF THE WEIGHT OF WORKER BEES ON DIVISION OF LABOR[1]

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It is widely believed that honeybees (*Apis*) and the tropical stingless honeybees (Meliponini) arose from bees similar in many ways to bumblebees (*Bombus*). In the latter group workers vary enormously in size within a colony while in *Apis* and the Meliponini, some controlling mechanism leads to reduced variances among mature workers, which are therefore of relatively uniform size.

Division of labor in bumblebees is strongly related to weight among individual bees. Heavier workers of *Bombus agrorum* Fabricius, for example, leave the colony earlier than medium-sized bees, and some of the lighter ones may never leave the colony during their whole life (Brian, 1952). In *Melipona quadrifasciata* Lep. division of work is strongly determined by the age of the bee and, to some extent by the needs of the colony (Kerr and Santos-Neto, 1953, 1956). *Trigona (Scaptotrigona) xanthotricha* Moure, which is a very highly evolved meliponine, has a division of labor influenced especially by age and, also, to a great extent by the needs of the colony (Hebling, Kerr, and Kerr, 1963). The same is true of *Apis* (Rösch, 1925, 1927, 1930; Lindauer, 1953).

Division of labor is one of the structural aspects of social polymorphism in insects (Michener, 1961). Practically all the evolution of social life in insects is based on the acquisition of social polymorphism; therefore, it is very important to learn the details of division of labor. The purpose of this study was to learn if the weight of workers of *Apis mellifera* has any influence in division of labor in that insect, as it presumably did in ancestral *Bombus*-like forms.

METHODS

Two different hives of *Apis mellifera adansonii* were used in this experiment. These bees were introduced to Brazil in 1956 from Tabora, Tanganyika, and Pretoria, South Africa. To avoid the influence of season, one experiment was done in the winter (June to July) and the other in the summer (December to February).

On June 1, 1960, one frame with workers and queen was transferred to an observation hive; another frame with emerging brood was put in an incubator at 36° C. Immediately after emergence, worker bees were collected, weighed, numbered, smeared with honey, and dropped into the observation hive mentioned above. Three days later they were observed. The following bees had been accepted (the numbers are for recognition of individuals in the hive):

	Bee number	Bee weight
1st class light bees	1	81.2 mg
	4	81.5 mg
	559	81.8 mg
	5	88.3 mg
	446	86.2 mg
2nd class medium-weight bees (discarded)	16	89.8 mg
	50	99.0 mg
	436	100.4 mg
3rd class heavy bees	300	101.9 mg
	348	102.0 mg
	434	106.2 mg
	318	106.5 mg
	10	107.2 mg
	18	109.2 mg
	304	110.0 mg
	333	110.4 mg

The bees weighing between 86.2 mg and

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101.9 mg were discarded. The bees were observed at least 4 hours a day (see table 1).

On December 26, 1960, another frame, with queen and workers from another hive of *Apis mellifera adansonii*, was placed in the observation hive. Twenty-nine bees were weighed and divided into three classes (these bees are referred to in table 2):

	Bee number	Bee weight
1st class light bees	121	78.8 mg
	130	89.6 mg
	110	90.6 mg
	155	92.2 mg
2nd class medium-weight bees (discarded)	149	94.4 mg
	156	94.4 mg
	152	95.2 mg
	128	96.3 mg
	137	96.6 mg
	111	96.8 mg
	154	96.9 mg
	119	97.3 mg
	104	98.2 mg
	118	98.2 mg
	181	99.0 mg
3rd class heavy bees	226	111.2 mg
	242	111.4 mg
	204	111.6 mg
	202	111.8 mg
	256	111.8 mg
	205	112.2 mg
	220	113.4 mg
	201	113.8 mg
	211	109.5 mg
	233	115.2 mg
	222	115.8 mg
	258	119.6 mg
	203	120.0 mg
	299	123.6 mg

As one can see in this second experiment all light bees received a number between 100 and 199 and all heavy bees a number between 200 and 299. This made distinction easier since bees of the first group received a white spot in the thorax and heavy bees received a red spot. In this second experiment the bees weighing between 92.2 mg and 111.2 mg were discarded. All bees were weighed soon after emerging: the time difference between the younger and the older individuals was less than 4 hours. All numbered bees were smeared with honey, introduced into the hive, and observed 8 hours a day.

Results

In the winter experiment we observed six different types of labor carried out by the worker bees: nursing larvae, receiving nectar, dehydration of nectar, courtship of the queen, attending communication dances, and field work.

In the summer experiment the observations were made taking the following "jobs" into consideration: cleaning themselves, cleaning cells, nursing old larvae, nursing young larvae, courtship of the queen, putting jelly around eggs, collecting honey from a feeding place, receiving nectar, closing of cells, attending communication dances, cleaning the hive, field work, dancing.

Winter experiment.—A summary of the observations is given in table 1. As one can see, all the jobs began to be carried out earlier by heavy bees than by light ones. Differences were as follows:

Nursing larvae—1 day ahead
Receiving nectar—1 day ahead
Attending communication dance—12 days ahead
Dehydration nectar—3 days ahead
Courtship of the queen—1 day ahead
Field work—7 days ahead

Summer experiment.—A summary of

TABLE 1. *Results of the winter experiment. Ages at which the bees began certain types of work*

Type of labor	Light bees		Heavy bees	
	Number	Age	Number	Age
Nursing larvae	1	5th day	318	4th day
Receiving nectar	559	8th day	348	7th day
Attending dance	5	20th day	300	8th day
Dehydrating nectar	1	11th day	10	8th day
Courtship of the queen	4	14th day	304	13th day
Field work	5	28th day	434	21st day

TABLE 2. *Result of the summer experiment. Ages at which the bees began certain types of work*

Labor	Light bees		Heavy bees	
	Number	Age	Number	Age
1. Cleaning themselves	130	1st day	220	1st day
2. Cleaning cells	156	2nd day	203	1st day
3. Nursing old larvae	156	5th day	203	4th day
6. Nursing young larvae	156	8th day	202	7th day
4. Courtship of the queen	130	7th day	203	4th day
7. Putting food around eggs	110	9th day	202	8th day
8. Collecting honey from a feeding place	156	10th day	204	8th day
9. Receiving nectar	–	–	299	10th day
5. Sealing brood cells	152	15th day	226	4th day
10. Attending communication dance	149	22nd day	205	17th day
12. Cleaning the hive	130	23rd day	201	21st day
11. Field work	110	27th day	205	18th day
13. Communication dance	149	28th day	226	22nd day

this experiment is given in table 2. Again, all the types of labor were first begun by the heavy bees; in no case did light bees start working at a new job ahead of the heavier ones, as one can see below:

Cleaning cells—1 day ahead
Nursing old larvae—1 day ahead
Nursing young larvae—1 day ahead
Queen courtship—2 days ahead
Putting food around eggs—1 day ahead
Collecting honey which was put in a feeder inside the hive—2 days ahead
Receiving nectar from field bees—no marked light bee was seen receiving nectar in this experiment
Sealing brood cells (before the old larvae spun the cocoon)—11 days ahead
Attending communication dances—5 days ahead
Cleaning the hive (putting wastes outside the hive)—2 days ahead
Field work—9 days ahead
Performing communication dance—6 days ahead

Discussion

In all cases in these two experiments heavy bees began new activities earlier than light bees. The probability of these results being by chance is smaller than 1 : 200,000, so we are safe in concluding that weight is still an important factor in determining the division of labor in *Apis mellifera*, notwithstanding the importance of age and the needs of the colony. The importance of weight in the division of labor may be considered as due to a constellation of genes that this species has in common with *Bombus*, or in other words, to relict factors from its common ancestry with bumblebees. It might have been a matter of chance but it is worth mentioning the fact that the bees performed communication dances 1 to 6 days after leaving the hive for field work; communication marks by *Trigona postica* workers were made 10 days after they began field work (Hebling, Kerr, and Kerr, 1963). A higher degree of nerve cell specialization and probably of training seems to be necessary to do certain types of jobs, which are thus carried out later in the life of the bee.

Comparing the weight of the brain of a light and a heavy bee, the following data were obtained: a bee weighing 69.8 mg had a brain with 1.8 mg, a bee weighing 95.8 mg had a brain of 2.3 mg. This may be the anatomical basis upon which our conclusions rest.

Summary

Bumblebees have a division of labor based upon the weight of the individual bee. In *Melipona quadrifasciata*, *Trigona xanthotricha*, and *Apis mellifera* the division of labor among workers is related to the age of the bee and, to a certain extent, to the needs of the hive (less in *Melipona*, more in *Trigona* and *Apis*). The present study demonstrated that weight is still important in relation to division of labor in *Apis mellifera*, since in two different experiments, the heavier bees changed to an

ontogenetically more advanced type of work earlier than the light bees.

LITERATURE CITED

BRIAN, A. D. 1952. Division of labor and foraging in *Bombus agrorum* Fabricius. J. Anim. Ecol., **21**: 223–240.

HEBLING, NILTON JOSÉ, WARWICK E. KERR, AND FLORENCE KERR. 1963. Divisão de trabalho entre operárias de *Trigona (Scaptotrigona) xanthotricha* Moure. Arq. Dept. Zoologia (in press).

KERR, W. E., AND G. R. DOS SANTOS NETO. 1953. Contribuição para o conhecimento da bionomia dos Meliponini. II. Divisão de trabalho entre as operárias de *Melipona quadrifasciata* Lep. Ciência e Cultura, **5**(4): 224–225.

—— AND ——. 1956. Contribuição para o conhecimento da bionomia dos Meliponini. V. Divisão de trabalho entre operárias de *Melipona quadrifasciata quadrifasciata* Lep. Insectes Sociaux, **3**: 423–430.

LINDAUER, M. 1953. Division of labour in the Honey Bee colony. Bee World, **34**: 63–73, 85–90.

MICHENER, C. D. 1961. Social polymorphism in Hymenoptera. *In* Insect polymorphism, J. S. Kennedy (ed.), p. 43–56. Royal Ent. Soc., London.

RÖSCH, G. A. 1925. Untersuchungen über die Arbeitsteilung in Bienenstaat. I. Z. Vergl. Physiol., **2**: 571–631.

——. 1927. Ueber die Bautätigkeit in Bienenvolk und das Alter der Baubienen. Z. Vergl. Physiol., **6**: 264–298.

——. 1930. Untersuchungen über die Arbeitsteilung in Bienenstaat. II. Z. Vergl. Physiol., **12**: 1–71.