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# THE ONTOGENY OF A DOMINANCE HIERARCHY IN COLONIES OF THE BUMBLEBEE *BOMBUS TERRESTRIS* (HYMENOPTERA, APIDAE)

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## *SUMMARY*

We investigated the ontogeny of the social structure in relation to the reproductive success of its members in four colonies of the bumblebee *Bombus terrestris* L. In all four colonies, the time of colony development was divided into four periods. Only in the last period did worker-oviposition occur.

For analysing the social structure of the nests, we used the same methods as used earlier by v. Honk & Hogeweg (1981), in order to test their results, which were based on one colony only. Our results confirm theirs in :

1. There exists a social hierarchy during all periods of colony development, in which the queen is always in the $\alpha$-position.

2. Dominance behaviour is positively correlated with activity (i.e. the number of interactions of a bee) in the nest.

3. A number of the workers present in each period hold a position in the hierarchy close to the queen. These workers are called elite workers. They show a characteristic behavioural pattern, in which egg laying by the elite workers occurs in the last period of colony development.

However, contrary to their findings we observed :

1. The proportion of elite workers varies from one period to another and from one colony to another, but is always less than 1/2 and generally decreases during colony development.

2. The growth rate of our colonies is significantly larger.

3. Only 33 % of the workers which reach an elite position in one of the first periods, remain in such position through the last period. The dropping of the other 67 % appears

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to be due to age and foraging: foragers quickly drop to a low position in the social hierarchy. Stability of the elite group is probably also related to the growth rate of the colonies.

4. Workers which emerge more than three days after the onset of the last period (i.e. after the start of worker egg laying) have no more chance of becoming elite workers.

Not withstanding the extensive egg laying activity of the elite workers, their reproductive success is small; the queen eats most of the worker-laid eggs. Since, moreover, the queen starts to lay unfertilized eggs before the workers start to oviposit, she has the parentage of most of the males.

Some possible reasons for the queen's 'switch' to the production of unfertilized eggs and for the start of worker egg laying are discussed.

## *ZUSAMMENFASSUNG*

### **Die Entwicklung der Dominanzhierarchie bei der Hummelart** Bombus terrestris

In 4 Kolonien der Hummelart *Bombus terrestris* L. wurde die Entstehung der sozialen Struktur und der Fortpflanzungserfolg von Königin und Arbeiterinnen untersucht. Die Entwicklung der Kolonien wurde in 4 Perioden unterteilt. Nur in der letzten Periode legten Arbeiterinnen Eier.

Für die Untersuchungen zur sozialstrucktur der Völker wurden die Methoden von v. Honk & Hogeweg (1981) verwendet, um ihre Ergebnisse, die an nur einem einzigen Volk erzielt wurden, zu überprüfen. Unsere Ergebnisse bestätigen folgendes:

1. In allen Perioden existiert eine Dominanzhierarchie, an deren Spitze die Königin steht.

2. Dominanzverhalten ist positiv mit der Aktivität im Nest (Anzahl der Interaktionen) korreliert.

3. In jeder Periode nehmen einige Arbeiterinnen einen Rang in der Hierarchie nahe der Königin ein. Sie werden 'Elite Arbeiterinnen' genannt und sind durch spezifische Verhaltensweisen characterisiert. Arbeiterinnen, die dauernd der Elitegruppe angehören legen in der letzten Periode der Volksentwicklung Eier.

Im Gegensatz zu v. Honk & Hogeweg (1981) fanden wir jedoch:

1. Der prozentuale Anteil dieser Arbeiterinnen kann in den einzelnen Kolonien und in den verschiedenen Perioden unterschiedlich sein; er ist aber immer kleiner als 1/2 und nimmt in der Regel während der Volksentwicklung ab.

2. Die Wachstumsrate unserer Völker ist signifikant größer.

3. Nur 33 % derjenigen Arbeiterinnen, die während der ersten 3 Perioden die Elitegruppe erreichen, befinden sich auch noch am Ende der 4. Periode darin. Die restlichen Arbeiterinnen fallen in der Hierarchie, weil sie entweder zu alt sind oder zu sammeln beginnen; Sammlerinnen nehmen innerhalb kurzer Zeit einen niedrigen Rang ein. Die Stabilität der Elitegruppe hängt wahrscheinlich auch von der Wachstumsgeschwindigkeit des betreffenden Volkes ab.

4. Arbeiterinnen, die erst in der 4. Periode schlüpfen, nachdem ältere Arbeiterinnen mit der Eiablage begonnen haben, können nicht mehr die Elitegruppe erreichen.

Obwohl Elite Arbeiterinnen häufig Eier legen, bleibt ihr Fortpflanzungserfolg gering; die Königin frißt alle Eier, die von Arbeiterinnen gelegt wurden. Sie beginnt mit der Ablage von Drohnen-Eiern bevor die Arbeiterinnen anfangen Eier zu legen, so daß die meisten Drohnen von ihr abstammen.

Mögliche Gründe für den Wechsel von der Ablage besamter zur Ablage unbesamter Eier der Königin sowie für den Beginn der Eiablage der Arbeiterinnen werden diskutiert.

## INTRODUCTION

Van HONK & HOGEWEG (1981) studied the existence and the changes in the dominance hierarchy in an intact colony of the bumblebee *Bombus terrestris* L. They were able to relate egg laying by the workers to their position in this hierarchy. At all stages of colony development a group of dominant workers (called elite workers) was found, comprising about one quarter of the worker population present at such a stage. Almost all of the workers that entered the elite group remained members of this group and became egglayers in the last period.

However, their analysis was based on one laboratory colony, that was kept imprisoned in a dark room and had only a limited number of workers. We, therefore, felt it necessary to repeat the observations and use more natural conditions.

Van DOORN & HOGEWEG (1985) analysed the behaviour of elite workers: they position themselves more often near the queen, where they will buzz more often than do other workers; they are principally the workers that lay eggs and/or show forms of behaviour associated with egg laying, and they are principally the workers that are attacked by the queen or are aggressive themselves towards the queen and each other, especially during the last period of colony development.

In the present paper we analyse the interaction behaviour of the queen and various groups of workers in detail.

## MATERIALS AND METHODS

### 1. Colony rearing

The basic technique of colony rearing was similar to that used by v. HONK & HOGEWEG (1981). However, there seem to have been some unintentional but crucial differences: the growth rate of our colonies is significantly larger than that of their nest. The maximum number of workers in their nest was 100, while in our nests the number of workers varies from 200 to 300, which is a more natural figure. Therefore a detailed account of colony rearing is given here: Four colonies were studied: A, B, C and D. The queens of colonies A (= T 81-1 in v. DOORN & HOGEWEG, 1985), C and D were captured shortly after hibernation in the Würzburg area. The queen of colony B (= T 81-2 in v. DOORN & HOGEWEG, 1985) had been produced by another laboratory colony, mated in confinement, and treated with $CO_2$ (RÖSELER & RÖSELER, 1984) to prevent her going into hibernation. Some of the queens which have been treated with $CO_2$ produce, along with the workers, a number of males intermittently. So did queen B. These males were taken out immediately. Each queen was placed in a wooden nestbox (9 $dm^3$), which was connected to a glass-covered outer compartment (7 $dm^3$), in a climate room (27°C; 60-70 % RH; light-dark = 18-6 hours). Queen A started her colony on her own, while in the case of the colonies B, C and D the queen was provided with male pupal comb (to stimulate egg laying) and some workers from other colonies. The males emerging from these pupae were removed immediately after emergence. The added workers were removed once the first batch of offspring of these queens had pupated.

From the emergence of the first workers onwards the climate room was kept in complete darkness.
Twice a day newly hatched workers were given identity tags (Opalithplättchen) on their thoraces.

In addition to the unintentional differences there were some intentional ones :
The outer compartment of colonies B and C were connected to a *flight cage* in the neighbouring room by means of a darkened tube, 2.5 cm in diameter and about 2.5 m long. In this flight cage the bees could collect diluted honey (water : honey = 2:1), that was offered in small portions scattered over the daylight period (the neighbouring room had daylight) to stimulate a steady foraging activity. Colony A got the diluted honey in the outer compartment (i.e. in the darkened climate room). The colonies A, B and C were fed pollen ad libitum, given directly into the nest and exchanged for fresh twice a day.
The workers of colony D were allowed to *go outside* through a 3 m long tube and a hole in the outer wall of the neighbouring room. This colony was self-supporting.

## 2. Observational methods and data processing

*A*) The interactions between the bees were observed and the data processed in a way identical to that used by v. HONK & HOGEWEG (1981). The basic data are all encounters between bees in which one of the bees after antennation 'retreats' (v. HONK & HOGEWEG, 1981). These data were obtained by daily video recordings of half-hour periods. The data were expressed in terms of number of retreats/proceedings of each pair of bees in a period of colony development (see below).

V. HONK & HOGEWEG proposed six possible ways to measure dissimilarities between the bees. After some more tests, we decided to base our analysis on both activity index and dominance index (v. HONK & HOGEWEG, 1981, p. 113, point 6).

Thus, social groups of bees were generated by cluster analysis with Ward's clustering criterion (WARD, 1963) using as dissimilarities between the bees the dissimilarities of their interactions towards all other members in terms of dominance index (DI) and activity index (AI), i.e. as :

$$\sum_{\substack{k=1\\k\neq i\\k\neq j}}^{N} \left( \left| AI_{ik} - AI_{jk} \right| \Big/ \operatorname{MAX}_{\substack{l=1\\l\neq k}}^{N}(AI_{lk}) + \left| DI_{ik} - DI_{jk} \right| \Big/ \operatorname{MAX}_{\substack{l=1\\l\neq k}}^{N}(DI_{lk}) \right) \Big/ (2N-4)$$

where $AI_{ik} = R_{ik} + P_{ik}$ and $DI_{ik} = P_{ik} / AI_{ik}$ ; $R_{ik}$ is the number of retreats of i for k, $P_{ik}$ is the number of proceedings of i to k.

In this paper we emphasize the characterisations of the thus obtained groups : the dendrograms are therefore compressed so as to show only the relations of the social groups, and not of the individual members (see *fig. 2*). We detail the interaction differences between the social groups in terms of statistics of the interactions between the groups. Data are presented for the most 'typical' colony C, but conclusions hold for the other colonies as well.

Apart from the dendrograms we represented the social structure also using principal coordinate analysis according to GOWER (1966), yielding an ordering of the members along one axis.

Lumping of the data into periods of nest development was less straightforward in our nests, compared to v. HONK & HOGEWEG (1981), because of the faster and more continuous growth of our colonies. We decided on four periods : Generally, the first period covers the time during which only the workers that emerged from the first batch of brood are present; the second period covers the following stage of slow increase; the third period covers the time of exponential increase up to the moment at which the workers start to lay eggs; period four covers the time of worker egg laying. In period 3 of colony C and in period 4 of colony D we had gathered so much data that it became possible to split the period into 2 subperiods (a and b).

The observations were made by the first author, the data processed by the second author.

*B*) From the video recordings and from direct observations, made with increasing frequency from about 5 to 50 times a day in the course of colony development, especially in the colonies B, C and D, we extracted data on individuals involved in the following behaviours:

I. *Egg Laying* proper

II. *Behaviour patterns associated* with egg laying, i.e.:

1. constructing egg cells (or repairing damaged ones)
2. testing egg cells (a bee that is not actually laying eggs, but is positioned on the the egg cell as if it is doing so for only a few seconds)
3. opening egg cells (of completely, or only partly closed egg cells, whether or not filled with eggs)
4. inspecting egg cells (exclusively involving inspection with the antennae of partly closed egg cells; often in combination with 3)
5. closing egg cells (after egg laying, opening, inspecting, or without such preceding behaviour)
6. attempts to destroy egg cells and/or to steal eggs, while they are being laid by the queen or a worker
7. eating eggs.

III. *Aggressiveness* (head butting with mandibles agape, biting or grappling with another bee, pulling on wings or hairs, or attempts to sting).

IV. *Retinue behaviour and Buzzing* (workers can position themselves near the queen, perpendicular to her longitudinal axis; mostly they press their bodies against the comb; generally they antennate, but never lick, the queen; these workers may start vibrating their wings (*Buzzing*), each vibration lasting less than one second).

*C*. In all colonies the identity of those individuals that foraged was registered (*Foraging*). In colony A no clear distinction could be made between foragers and non-foragers, thus the registration was stopped after 4 weeks for that colony.

*D*. As soon as egg laying by workers had stopped, all observations were stopped: in colony A 16 days after the end of the last period of video recording, in B at the end of the last period, in C 2 days after the end and in colony D 8 days after the end of the last period. Some of the workers of colony D were then dissected to examine ovarian development.

## RESULTS

### 1. Growth Rate

*Figure 1* shows the increase in size of the worker population of the colonies. This differs considerably from one colony to another, but was always faster than in the colony of v. HONK & HOGEWEG (1981). No queens were reared in any of the colonies. In colony B males were produced intermittently during the increase of the worker population. This unusual phenomenon is due to the rearing method of bypassing diapause applied to queen B. Fifteen males preceded the first workers; a total of 143 males emerged in bursts of 12-24 before the start of worker egg laying and another 158 continuously along with workers during period 4. If all the males and workers are summed, the increase in size of colony B approximates that of colony C.

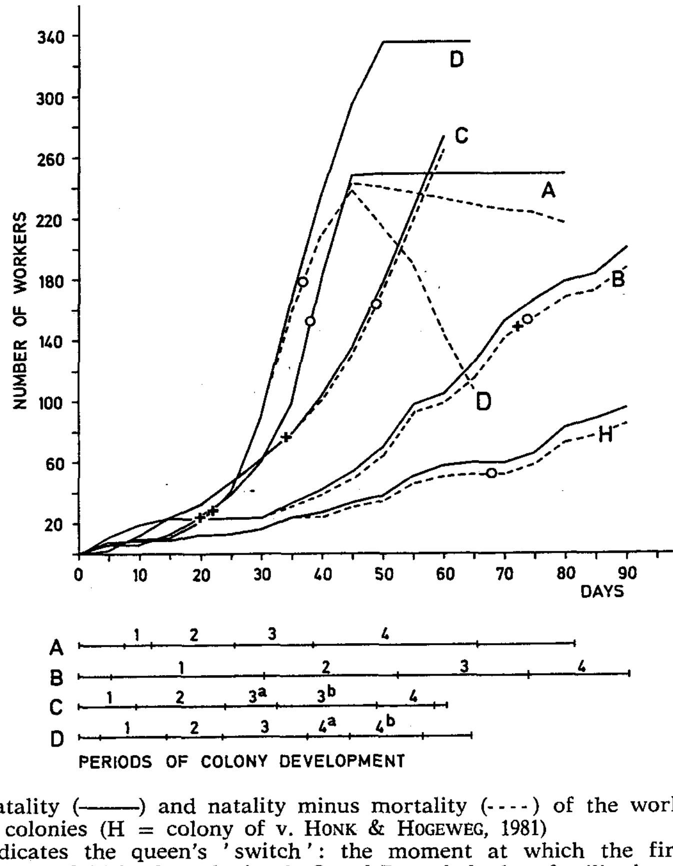


Fig. 1. — Natality (———) and natality minus mortality (- - - -) of the worker population of the colonies (H = colony of v. HONK & HOGEWEG, 1981)
× : indicates the queen's 'switch': the moment at which the first unfertilized eggs are laid in the colonies A, C and D, and the last fertilized eggs in colony B
O : indicates the start of worker egg laying.

Abb. 1. — Zunahme der Arbeiterinnen-Anzahl während der Entwicklung der Hummelvölker ohne Berücksichtigung der Mortalität (———) und unter Berücksichtigung (- - - -) (H = Kolonie von v. HONK & HOGEWEG, 1981)
× = Zeitpunkt, an dem Königin die ersten unbesamten Eier legte (Kolonie A,C,D), bzw. das letzte besamte Ei gelegt wurde (Kolonie B)
O = Zeitpunkt, an dem die Arbeiterinnen die ersten Eier legten.

*Figure 1* also shows that mortality was small in the colonies A, B and C, as in the colony of v. HONK & HOGEWEG (1981), but considerable in the free flying colony D, especially in the last period.

**2. Analysis of the Recorded Interactions**

2.1. SOCIAL GROUPS

*2.1.1. general description*

For each period a division of the worker population was obtained by cluster analysis, delimiting groups of bees that have a high degree of similarity with regard to their activity and dominance indices in comparison with the bees of oher groups (*fig. 2*) : the elite group (E), the common worker group (W) and the transition group (T) (see v. HONK & HOGEWEG 1981, pp. 115-116). In some cases the structure of E gave rise to a division into two groups which were clearly separated. In such cases we called one subgroup 'sub-elite' (E−), the other 'super-elite' (E+) (for criteria see below).

*2.1.2. special properties*

For each period, the mean activity and dominance indices of the members of the clusters in their interactions with each member of their own group and each member of the other groups was calculated. As a representative example the data of colony C are given (*table I*). Although most members of a group were similar in their activity and dominance indices, some deviated.

The calculations lead to the following general conclusions :

*a. the queen.* — The queen is the most active bee in the colony. Workers almost always retreat in encounters with the queen.

We calculated for the different periods of colony development the mean number of interaction per half-hour that the queen had with E-, T- and W-workers as groups, and contacts of individual E-, T- and W-workers with the queen (*table II*). It can be observed that with increasing time in all 4 colonies the queen, of course, becomes more involved in these interactions. In colonies A, B and D she clearly reached a maximum at the onset of period 4. As queen C was killed by elite workers at the onset of period 4, it is not possible to verify this in colony C. *Table II* also shows that the queen has the greatest number of interactions with E-workers, fewer with T-workers, and the least with W-workers. During colony development, however, the queen has a decreasing number of interactions per individual E-, T- or W-worker.

*b. the elite group (E).* — Like v. HONK & HOGEWEG (1981) we found that an E-worker has the highest number of interactions with E-workers, fewer with T-workers, and the least with W-workers, as is true of the queen. It as a positive dominance index (d.i. $>$ 0.5) over T- and W-

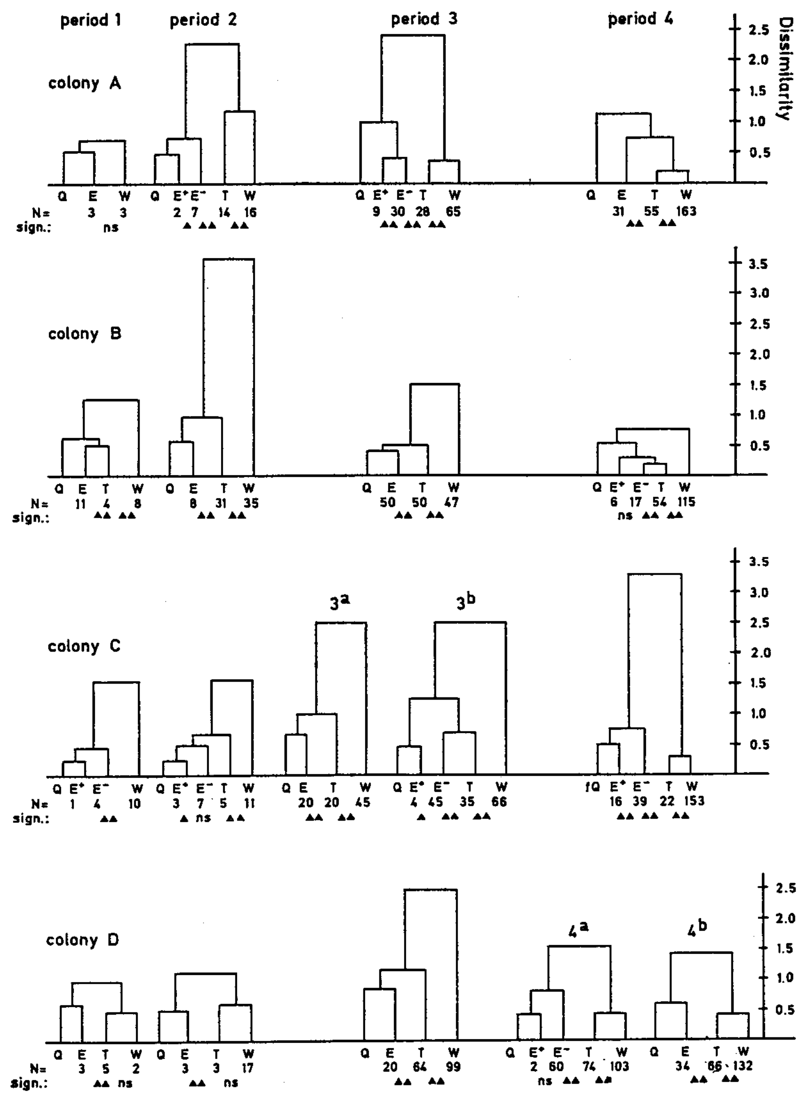


Fig. 2. — Dendrograms of the cluster analysis (CA) representing the social structure of the colonies (A,B,C,D) in four periods of nest development. The dendrograms were generated on data of all individual bees (see section 2A of M &M), but are here compressed to the level of " social groups ": splitting levels were choosen in which 3-5 groups were clearly separated (Q = queen, fQ = 'false queen', E = elite group, E+ = super-elite group, E− = sub-elite group, T = transition group, W = common worker group; N = number of bees belonging to the groups).
The results of the CA and the principal coordinate analysis (PCA) were compared by calculating the significance of the differences between the mean PCA-values of the workers of the social groups, using the t-test: ns = not significant, ▲ = $p < .05$, ▲▲ = $p < .01$.

workers. As has been mentioned earlier in some cases the elite group was separated in two subgroups, E+ and E−, by cluster analysis. The workers of E+ have higher activity and dominance indices than the workers of E−.

Most workers need a period of 7-15 days to become members of E. Only a few workers needed up to 3 weeks.

On average 58 % of the workers which become members of E are found in E in the next period. The rest (42 %) are then found in T or W. About 33 % of the workers which become members of E before the last period stay in this position up to the end of the last period. Therefore, the increase in the number of E (see *fig. 2*) is especially due to young bees.

Some of the E-workers disappear from E for the following reasons :

1. *Foraging.* — E-workers which had started to forage left E before the last period at the latest (in colony B 14 out of 44 workers which left E, in colony C 25 out of 38 workers which left E, and in colony D 46 of 58 workers which left E). All these workers went to W via T. A proportion of these workers which left E appeared to die before the video recordings ended (in colony B 2 out of 14, in colony C 3 out of 25, and in colony D 27 out of 46).

2. *Age.* — In colonies A, C and D about 33 % of the workers that had emerged in the first 4 weeks of colony development and had become members of E were still found in E in the last period, i.e. 2-3 weeks later. In colony B, however, none of these workers could still be found in E in the last period. In colony B the last period started more than 6 weeks later.

*c. the common worker group (W).* — W-workers are usually less active than other workers, and have a low dominance index. However, in the first period in all 4 colonies their activity level reaches that of the E-workers. In the first period in colonies A, B and C they have indeed a lower dominance index than the E-workers, but this was not found in colony D. Generally, they have most of their interactions with the queen, fewer with E-, even fewer with T-, and the least with other W-workers.

On average 40 % of the W-workers are found in W in the next period, 35 % in E and 25 % in T.

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Abb. 2. — Die Dendrogramme der Cluster Analyse (CA) zeigen die soziale Struktur der Kolonien (A,B,C,D) während der vier Perioden ihrer Entwicklung. Die Dendrogramme basieren zwar auf den Daten aller Hummeln (s. Abschnitt 2A von Material & Methode), die aber hier in die sozialen Gruppen zusammengefaßt wurden ; die Auftrennung wurde dort vorgenommen, wo 3-5 Gruppen klar getrennt waren (Q = Königin, fQ = 'Ersatz Königin', E = Elitegruppe, E + Super-Elitegruppe, E− = Sub-Elitegruppe, T = Uebergangsgruppe, W = Restgruppe ; N = Anzahl der Arbeiterinnen in den Gruppen).
Die Resultate der CA und der Principal Coordinate Analyse (PCA) wurden verglichen durch Berechnung der Signifikanz (t-Test) der Unterschiede zwischen den mittleren PCA-Werten der Arbeiterinnen der sozialen Gruppen ; ns = nicht signifikant, ▲ = $p < .05$, ▲▲ = $p < .01$.

Table I. — Characterisation of the social groups by means of the average activity index (AI) and the average dominance index (DI) per developmental period in the colony C. The upper right corners of the AI matrices have been left out because these matrices are symmetrical (Q = queen, fQ = 'false queen', E = elite group, E+ = super-elite group, E− = sub-elite group, T = transition group, W = common worker group ; further explanation : see text)

×××× = value not applicable (only one member)

N = group not present.

Tabelle I. — Charakterisierung der sozialen Gruppen durch den mittleren Aktivitäts-Index (AI) und den mittleren Dominanz-Index (DI) für jede Entwicklungsperiode in der Kolonie C. Die obere rechte Hälfte der AI-Matrizen wurde weggelassen, weil diese Matrizen symmetrisch sind (Q = Königin, fQ = 'Ersatz Königin', E = Elitegruppe, E+ = Super-Elitegruppe, E− = Sub-Elitegruppe, T = Uebergangsgruppe, W = Restgruppe ; weitere Erklärung : s. Text)

×××× = Wert nicht anzugeben, da diese Gruppe nur 1 Individuum enthält

N = Gruppe nicht vorhanden.

| Period | Activity index | | | | | | Dominance index | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Q | E+ | E− | T | W | | Q | E+ | E− | T | W |
| 1 | Q | ×××× | | | | | Q | ×××× | 0.07 | 0.05 | N | 0.01 |
| | E+ | 42.0 | ×××× | | | | E+ | 0.93 | ×××× | 0.43 | N | 0.13 |
| | E− | 25.0 | 21.0 | 15.2 | | | E− | 0.95 | 0.57 | 0.50 | N | 0.20 |
| | T | N | N | N | N | | T | N | N | N | N | N |
| | W | 15.0 | 11.1 | 7.3 | N | 3.6 | W | 0.99 | 0.87 | 0.80 | N | 0.50 |
| | | Q | E+ | E− | T | W | | Q | E+ | E− | T | W |
| 2 | Q | ×××× | | | | | Q | ×××× | 0.09 | 0.03 | 0.02 | 0.02 |
| | E+ | 25.7 | 18.3 | | | | E+ | 0.91 | 0.50 | 0,48 | 0.19 | 0.23 |
| | E− | 14.9 | 11.1 | 8.0 | | | E− | 0.97 | 0.52 | 0.50 | 0.25 | 0.28 |
| | T | 20.8 | 15.5 | 10.3 | 18.9 | | T | 0.98 | 0.81 | 0.75 | 0.50 | 0.53 |
| | W | 7.7 | 5.8 | 3.4 | 4.8 | 1.7 | W | 0.98 | 0.77 | 0.72 | 0.47 | 0.50 |
| | | Q | E | T | W | | | Q | E | T | W | |
| 3a | Q | ×××× | | | | | Q | ×××× | 0.01 | 0.03 | 0.00 | |
| | E | 15.2 | 6.5 | | | | E | 0.99 | 0.50 | 0.56 | 0.37 | |
| | T | 5.3 | 2.8 | 1.7 | | | T | 0.97 | 0.44 | 0.50 | 0.36 | |
| | W | 2.4 | 0.8 | 0.5 | 0.3 | | W | 1.00 | 0.63 | 0.64 | 0.50 | |
| | | Q | E+ | E− | T | W | | Q | E+ | E− | T | W |
| 3b | Q | ×××× | | | | | Q | ×××× | 0.04 | 0.02 | 0.02 | 0.00 |
| | E+ | 15.5 | 5.5 | | | | E+ | 0.96 | 0.50 | 0.35 | 0.30 | 0.16 |
| | E− | 7.5 | 2.9 | 1.0 | | | E− | 0.98 | 0.65 | 0.50 | 0.49 | 0.30 |
| | T | 4.2 | 1.7 | 0.8 | 0.7 | | T | 0.98 | 0.70 | 0.51 | 0.50 | 0.37 |
| | W | 1.8 | 0.7 | 0.3 | 0.1 | 0.1 | W | 1.00 | 0.84 | 0.70 | 0.63 | 0.50 |
| | | fQ | E+ | E− | T | W | | fQ | E+ | E− | T | W |
| 4 | fQ | ×××× | | | | | fQ | ×××× | 0.05 | 0.02 | 0.18 | 0,04 |
| | E+ | 17.1 | 9.6 | | | | E+ | 0.95 | 0.50 | 0.33 | 0.25 | 0.22 |
| | E− | 10.3 | 2.5 | 1.6 | | | E− | 0.98 | 0.67 | 0.50 | 0.40 | 0.35 |
| | T | 3.7 | 1.0 | 0.6 | 0.3 | | T | 0.82 | 0.75 | 0.60 | 0.50 | 0.47 |
| | W | 0.7 | 0.2 | 0.1 | 0.02 | 0.02 | W | 0.96 | 0.78 | 0.65 | 0.53 | 0.50 |

Table II. — Mean number of interactions of the queens with the workers per half-hour in the different periods of colony development (E = elite group, E+ and E– are taken together, T = transition group, W = common worker group; further explanation: see text) * = interactions of the 'false queen'.

Tabelle II. — Anzahl der Interaktionen zwischen Königinnen und den einzelnen Arbeiterinnen-Gruppen während der verschiedenen Perioden der Volksentwicklung. Aufgetragen sind die Mittelwerte pro 1/2 Stunde (E = Elitegruppe, enthält E+ und E–, T = Uebergangsgruppe, W = Restgruppe; weitere Erklärung: sehe Text) * = Interaktionen der 'Ersatz Königin'.

| Colony | Period | Interactions with | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | All the workers | All the members of | | | Individual members of | | |
| | | | E | T | W | E | T | W |
| A | 1 | 12.5 | 5.5 | — | 7.0 | 1.8 | — | 2.3 |
| | 2 | 16.0 | 9.1 | 4.7 | 2.2 | 1.0 | 0.3 | 0.1 |
| | 3 | 41.6 | 27.2 | 8.0 | 6.4 | 0.7 | 0.3 | 0.1 |
| | 4 | 41.2 | 23.3 | 9.6 | 8.3 | 0.7 | 0.2 | 0.05 |
| B | 1 | 18.6 | 10.7 | 3.2 | 4.7 | 1.0 | 0.8 | 0.6 |
| | 2 | 34.6 | 11.1 | 19.5 | 4.0 | 1.4 | 0.6 | 0.1 |
| | 3 | 41.3 | 26.2 | 12.3 | 2.8 | 0.5 | 0.2 | 0.1 |
| | 4 | 51.8 | 20.6 | 13.7 | 17.5 | 0.9 | 0.2 | 0.2 |
| C | 1 | 26.5 | 12.6 | — | 13.6 | 2.6 | — | 1.4 |
| | 2 | 34.5 | 16.4 | 9.4 | 8.7 | 1.6 | 1.9 | 0.8 |
| | 3a | 37.8 | 24.1 | 8.2 | 5.5 | 1.2 | 0.4 | 0.2 |
| | 3b | 44.3 | 26.6 | 9.7 | 8.0 | 0.5 | 0.3 | 0.1 |
| | 4* | 55.0 | 44.9 | 6.1 | 4.0 | 0.8 | 0.3 | 0.03 |
| D | 1 | 28.2 | 12.2 | 10.8 | 5.2 | 4.1 | 2.2 | 2.6 |
| | 2 | 42.3 | 12.8 | 5.7 | 23.8 | 4.3 | 1.9 | 1.4 |
| | 3 | 52.0 | 18.6 | 21.2 | 12.2 | 0.9 | 0.3 | 0.1 |
| | 4a | 68.5 | 42.1 | 19.0 | 7.4 | 0.7 | 0.2 | 0.1 |
| | 4b | 50.7 | 28.7 | 16.1 | 5.9 | 0.8 | 0.2 | 0.04 |

*d. the transition group (T).* — In the colonies A and D a number of the workers distinguish themselves from the W-workers by a higher activity, especially in interactions with E-workers, and by a somewhat higher, but nevertheless small, dominance index. We defined this group as transition group (T) (see also v. HONK & HOGEWEG, 1981, p. 115). In the colonies B and C a subgroup on the E-side of the first fork of the dendrogram (independent of the mentioned E-group) became discernible. The workers in this subgroup are about half as active as the other E-workers (including E–). Also their dominance index is clearly smaller. Moreover, they have a changeable position similar to that of the workers in the transition group of colonies A and D in that they were in E or W in the previous period and become members of E or W in the next period (*table III*). Therefore, we called this subgroup T as well.

Table III. — Inconstancy of the members of the transition group (T-workers) with regard to their position in the hierarchy in the developmental periods of the colonies (E = elite group, E+ and E− are taken together, T = transition group, W = common worker group; explanation in the text).

Tabelle III. — Die Entwicklung der hierarchischen Stellung der Arbeiterinnen der Uebergangsgruppe (T-Arbeiterinnen) in den verschiedenen Perioden der Volksentwicklung (E = Elitegruppe, enthält E+ und E−, T = Uebergangsgruppe W = Restgruppe; weitere Erklärung: sehe Text).

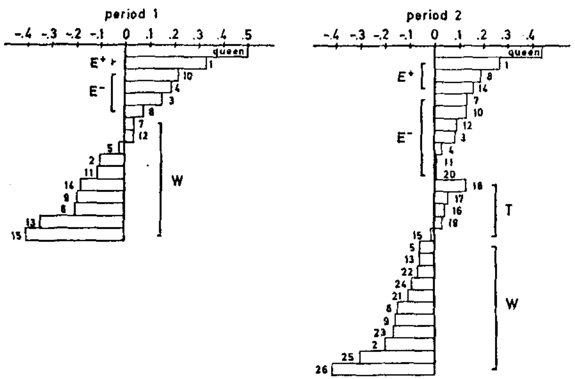
| Colony | Period | Number of T-workers | Position in the hierarchy: In the previous period | | | | Position in the hierarchy: In the next period | | |
|---|---|---|---|---|---|---|---|---|---|
| | | | Not yet born | In W | In T | In E | In E | In T | In W or not active |
| A | 2 | 44 | 13 | — | — | 1 | 12 | 2 | — |
| | 3 | 28 | 22 | 2 | 2 | 2 | 5 | 11 | 11 |
| | 4 | 55 | 14 | 21 | 11 | 9 | Not applicable | | |
| B | 1 | 4 | Not applicable | | | | 5 | 1 | 2 |
| | 2 | 31 | 25 | 1 | 1 | 4 | 9 | 11 | 10 |
| | 3 | 50 | 27 | 11 | 11 | 1 | 8 | 10 | 31 |
| | 4 | 54 | 8 | 16 | 10 | 20 | Not applicable | | |
| C | 2 | 5 | 4 | 1 | — | — | 5 | — | — |
| | 3a | 20 | 13 | 4 | — | 3 | 8 | 8 | 4 |
| | 3b | 35 | 7 | 12 | 8 | 8 | 6 | 4 | 24 |
| | 4 | 22 | 6 | 6 | 4 | 6 | Not applicable | | |
| D | 1 | 5 | Not applicable | | | | — | 1 | 4 |
| | 2 | 3 | 2 | — | 1 | — | — | 1 | 2 |
| | 3 | 64 | 50 | 12 | 1 | 1 | 9 | 9 | 46 |
| | 4a | 74 | 22 | 40 | 9 | 3 | 8 | 14 | 52 |
| | 4b | 66 | 27 | 13 | 14 | 12 | Not applicable | | |

On average 22 % of the members of T are found in T in the next period, 30 % in E and 48 % in W.

The fact that the group-division of the subperiods, into which period 3 of colony C and period 4 of colony D are divided, fits so well into general scheme confirms the correctness of the described division of the worker population.

### 2.2. Hierarchical system

A principal coordinate analysis (PCA) reveals an ordering of the workers above and below ' a mean level activity and dominance index. For all colonies the PCA supports the groupings that are generated by the cluster analysis, if the mean PCA-values of the workers of the different groups are compared. In almost all cases the differences between the mean values are significant at the $p < .01$ level (t-test) (see *fig. 2*, and compare also *fig. 3*). Within the elite group, i.e. between E+ and E−, the differences are smaller and in many cases not significant.



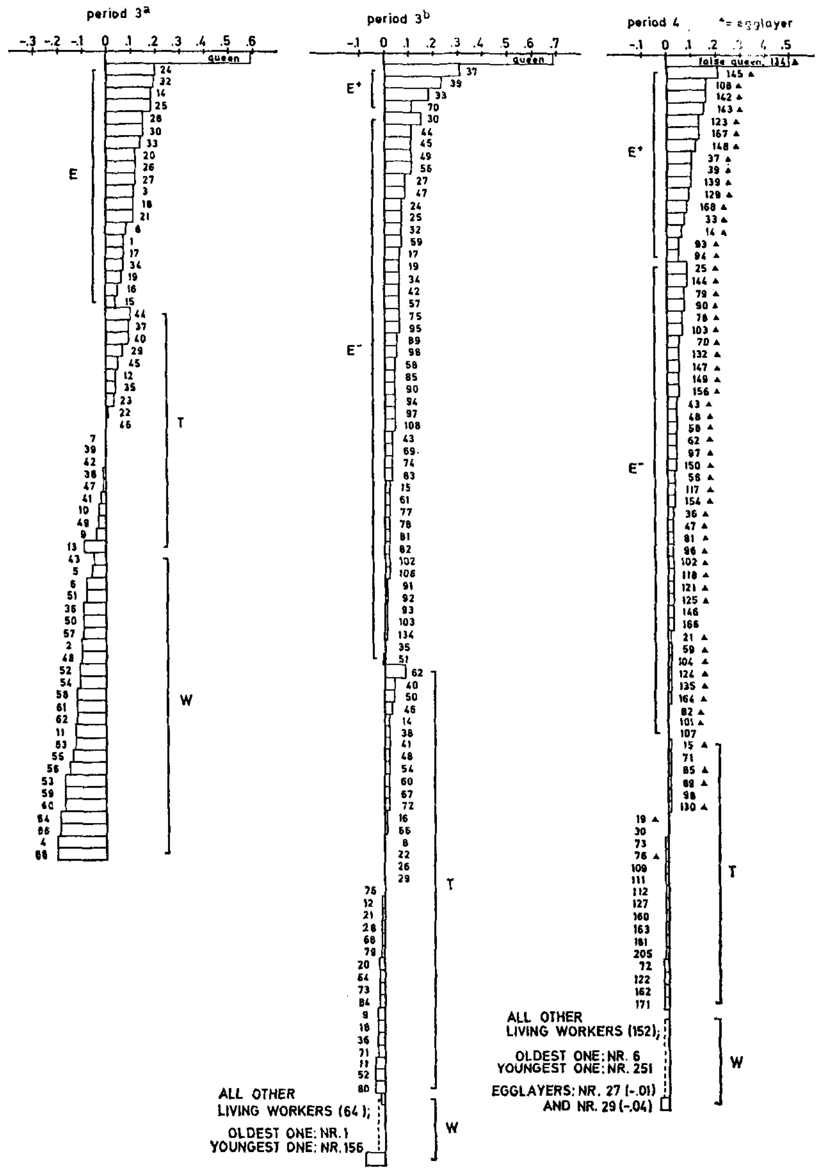




Fig. 3. — Social structure of colony C in the subsequent periods of its development. The position on the first principal coordinate (which can be interpreted as 'hierarchical ladder') of each bee is depicted. The bees are ordered according to the social groups generated by cluster analysis (see *fig. 2, C*). Numbers of bees indicate relative age.

Abb. 3. — Sozialstruktur der Kolonie C wärend der einzelnen Perioden ihrer Entwicklung. Die Position jeder Hummel auf der ersten Principal Coordinate (welche als 'hierarchische Leiter' interpretiert werden kann) ist angegeben. Die Individuen sind nach den sozialen Gruppen geordnet, die sich aus der Cluster Analyse ergeben haben (s. *Abb. 2, C*). Die Nummern der Hummeln geben das relative Alter an.

The queen is always at the top of the hierarchy (in colony C, period 4, after the death of the queen, replaced by the 'false queen'). The 'above average' section of the worker population appears to vary from one colony to another, ranging from 1/4 to 1/2. In colony D the 'above average' section is generally smaller than in the other colonies. No clear linear hierarchical structure could be established among the workers as many bees appeared to have approximately the same value, especially at the lower end of the PCA-scale. Therefore, we think that the hierarchy has a pyramidal rather than a linear structure. An example, using colony C, is given in *figure 3*.

### 3. Details of the Behavioural Observations

#### 3.1. Retinue behaviour and buzzing

Retenue behaviour and buzzing were investigated in colonies B, C and D. Generally, the E-workers of the colonies positioned themselves near the queen and in almost all periods buzzed more often than T-workers ($p < .01$) ; T-workers differed significantly from the W-workers (see also v. Doorn & Hogeweg, 1985).

As already mentioned, workers become members of E at the earliest at 7-15 days of age. We estimated the frequencies of both types of behaviour in the first 10 days of worker life, to investigate whether these future E-workers already distinguished themselves from the other workers before the moment of entering E. This is indeed the case (*table IV*).

Table IV. — Difference in the frequency of retinue and buzzing behaviour of future elite workers and non-elite workers during the first 10 days of their lives ($\bar{X}$ = mean number of days on which the behaviour was observed, sd = standard deviation, ns = not significant).

Tabelle IV. — Unterschiede in der Häufigkeit des Hofstaat- und Schwirrverhaltens zwischen künftigen Elite Arbeiterinnen und Nicht-Elite Arbeiterinnen während der ersten 10 Lebenstage ($\bar{X}$ = mittlere Anzahl der Tage, an denen das Verhalten beobachtet wurde, sd = Standard Abweichung, ns = nicht signifikant).

| Behaviour | Colony | Future elite workers | | | Future non-elite workers | | | t-test |
|---|---|---|---|---|---|---|---|---|
| | | N | $\bar{X}$ | sd | N | $\bar{X}$ | sd | |
| Retinue | B | 70 | 3.8 | 2.1 | 110 | 2.7 | 1.8 | $t = 3.5$ ; $p < .01$ |
| | C | 61 | 3.1 | 1.8 | 41 | 2.2 | 1.6 | $t = 2.4$ ; $p < .05$ |
| | D | 44 | 3.1 | 2.0 | 85 | 1.1 | 0.9 | $t = 6.3$ ; $p < .01$ |
| Buzzing | B | 70 | 0.9 | 1.3 | 110 | 0.6 | 1.2 | $t = 1.4$ ; ns |
| | C | 61 | 1.0 | 1.3 | 41 | 0.4 | 0.8 | $t = 2.9$ ; $p < .01$ |
| | D | 44 | 1.5 | 1.5 | 85 | 0.4 | 0.7 | $t = 4.6$ ; $p < .01$ |

### 3.2. Aggressiveness

In all 4 colonies aggressiveness was almost exclusively seen around the time at which worker egg laying started (period 4), and most of the aggression was restricted to a period of about 10 days. *Table V* presents data for colony C. The table shows that being aggressive and being attacked are strongly correlated with egg laying. Within the group of egglayers the number of attacks (performed or received) is strongly correlated with the number of ovipositions observed per bee (in colony C corr. = .36 and .72 resp.).

Table V. — Relation between egg laying and aggressiveness in colony C (period 4)
* = excluding the 'false queen'.

Tabelle V. — Beziehung zwischen Eiablage und Aggressivität während der Periode 4 in der Kolonie C
* = ohne 'Ersatz Königin'.

| | Total | Aggressive ones | Number of their attacks | Attacked ones | Number of attacks on them |
|---|---|---|---|---|---|
| Egglayers * | 60 | 22 | 253 | 60 | 675 |
| Non-egglayers | 169 | 9 | 15 | 51 | 121 |
| 'False queen' | 1 | 1 | 429 | 1 | 1 |

There were some differences between the colonies. In colony A the queen was the most aggressive bee (122 of 198 attacks), and was never seen to be attacked by the workers. In colony B, however, the queen was attacked herself (134 of 146 attacks), but remained alive and active on the comb. In colony C the queen was attacked and killed by several elite workers (113 of 223 attacks observed up to her death) ; thereafter a 'false queen' emerged: a worker which was the most aggressive bee and which was attacked herself only once (*table V*). In colony D very little aggression could be observed (only 17 attacks). The queen was attacked 8 times. She remained alive and active on the comb.

### 3.3. Egg laying and behaviour patterns associated with egg laying

In all 4 colonies a clear positive correlation exists between the number of observed ovipositions of each bee and her position in the hierarchy, as expressed by her PCA-value (corr. = .49, .41, .59 and .67 in the colonies A,B,C and D resp.).

In all colonies almost all workers that belonged to the elite group in the last period laid eggs. In *table VI* the example of colony C is presented. The percentage of newly-emerged workers that become members of E for at least one period generally decreases during colony development and even

Tabe VI. — Relation between the moment of emergence (subsequent weeks of colony development) and

a) reproductivity and position in the hierarchy (i.e. membership of the elite group (E, E+ and E− are taken together)),

b) the position in the hierarchy of the (egglaying) workers in period 4 (E = elite group, T = transition group, W = common worker group; for explanation: see text)

in colony C (at some time in E: in E for at least one period; →: indicates the start of worker egg laying).

Tabelle VI. — Beziehungen zwischen dem Zeitpunkt des Schlüpfens während der aufeinander folgenden Wochen der Volksentwicklung und

a) der Eiablage der Arbeiterinnen und ihrer Zugehörigkeit zur Elitegruppe (E, enthält E+ und E−),

b) der Zugehörigkeit der (eilegenden) Arbeiterinnen zu den Dominanzgruppen in der Periode 4 (E = Elitegruppe, T = Uebergangsgruppe, W = Restgruppe; weitere Erklärung: sehe Text)

in der Kolonie C (at some time in E: mindestens eine Periode in E; →: bezeichnet den Beginn der Eiablage der Arbeiterinnen).

| a) | Week | Total emerged | Egglayers | % egg-layers | At some time in E | % at some time in E | Egglayers at some time in E |
|---|---|---|---|---|---|---|---|
| | 1 | 14 | 1 | 7 | 9 | 64 | 1 |
| | 2 | 8 | 3 | 37 | 7 | 87 | 3 |
| | 3 | 10 | 4 | 40 | 8 | 80 | 3 |
| | 4 | 28 | 9 | 32 | 18 | 64 | 9 |
| | 5 | 19 | 6 | 32 | 9 | 47 | 5 |
| | 6 | 40 | 16 | 40 | 22 | 55 | 15 |
| | 7 | 60 | 22 | 37 | 22 | 37 | 21 |
| → | 8 | 64 | 0 | 0 | 0 | 0 | 0 |
| | 9 | 41 | 0 | 0 | 0 | 0 | 0 |
| | 10 | 0 | — | — | — | — | — |

| b) | Emerged in week | Position in the hierarchy in period 4 | | | | | |
|---|---|---|---|---|---|---|---|
| | | All workers | | | Egglayers only | | |
| | | In E | In T | In W or inactive | In E | In T | In W or inactive |
| | 1 | 1 | 0 | 13 | 1 | 0 | 0 |
| | 2 | 1 | 2 | 5 | 1 | 2 | 0 |
| | 3 | 2 | 1 | 7 | 2 | 0 | 2 |
| | 4 | 9 | 0 | 19 | 9 | 0 | 0 |
| | 5 | 5 | 4 | 10 | 5 | 1 | 0 |
| | 6 | 15 | 7 | 18 | 14 | 2 | 0 |
| | 7 | 22 | 8 | 30 | 21 | 1 | 0 |
| → | 8 | 0 | 1 | 63 | 0 | 0 | 0 |
| | 9 | 0 | 0 | 41 | 0 | 0 | 0 |

becomes zero shortly after the start of worker egg laying. At the same time the percentage of newly-emerged workers that lay eggs becomes zero (*table VI*).

All egglayers appeared to show one or more of the behaviour patterns associated with egg laying more than once. Furthermore, in all colonies some workers were found which did not lay eggs, but did show these forms of behaviour. Among them were almost all non-egglaying elite workers of the last period (N = 9,9,1,1 in colonies A, B, C and D resp.). The rest of these workers were either found in T (N = 9,13,1,3) or in W (N = 8,5,3,17). We dissected 13 of such workers from colony D. They all had developed ovaries (biggest oocyte ranging from 1.7 to 3.5 mm ; ripe eggs measure about 3.5 mm). Except in the 2 youngest workers among them, we found degenerated material in front of the first intact oocyte in their ovaries. Therefore, we must conclude that possibly some of them had laid eggs at an earlier time without having been discovered.

In colony A the youngest workers to lay eggs were 8 days old ; in colony B 15 days ; and in the colonies C and D they were 7 days old.

### 3.4. Foraging

From the colonies B and C, foraging in a flight cage, 16 % (N = 33) and 23 % (N = 57) respectively of the workers were seen to forage ; in the free flying colony D 51 % (N = 169) of the bees foraged. On average the bees of colony D started to forage on the 5th day of life ($X = 5.1 \pm 1.5$). This is clearly earlier than was found in the colonies B and C ($8.3 \pm 4.8$ and $8.9 \pm 3.8$ respectively).

On average those foragers of colony D that had emerged in the first 3 periods of colony development lived only $19.9 \pm 6.2$ days (N = 132). In the colonies B and C almost all of them lived at least 45 days ; only some of the oldest foragers had died.

Generally, foragers were found in all groups. The foragers' highest position in the hierarchy with respect to the whole period of colony development, measured as the distribution over E, T and W, did not differ from those of the housebees in colonies C and D, but differed in colony B : the E-position is under-represented, and the W-position is over-represented ($X^2$ - test, $p < .01$). Since in colony B the periods had a long duration (see *fig. 1*) as compared to colonies C and D, and since foraging E-workers leave E after a short time, it is possible that in colony B many foraging E-workers are not recognized as such. No difference could be observed in the age at the start of foraging between foragers that had been members of E, T or W for some time. In all 3 colonies most of the foragers were recruited before the onset of the last period ; those which were recruited during the last period did not become members of E. Since, moreover, all older foragers had already dropped to, or still were at, a low position in the hierarchy, no foragers were members of E in the last period. In accordance with this point no forager was observed to lay eggs. In colony D we dissected 3 foragers during period 3, 11 in period 4, and 17 after period 4. Most of them had only slightly developed ovaries (biggest oocyte $< 1.2$ mm).

## DISCUSSION

### The Ontogeny of Colony Structure

The analysis of the interaction structure between the workers and the queen, and among the workers, shows that in all periods of colony development the worker population varies in the activity of its members, and that these differences are mostly related to different dominance indices. A differentiation of more active and dominant workers, called elite workers, takes place. These workers become the egglayers in the last period of colony development. This confirms the results of v. HONK & HOGEWEG (1981).

The new element that can be added to this knowledge is that the dominance hierarchy can be very dynamic. In our colonies 67 % of the elite workers left their group (E) before the start of worker egg laying and did not lay eggs. The following reasons for this phenomenon were found: 1. *foraging*: all foraging E-workers left E; 2. *age*: E-workers appeared to remain members of E for a maximum of 8 weeks. Probably, at the same time, the growth rate of the colony plays a role: a higher growth rate causes greater competition from newly-emerging workers. The great dynamism of the hierarchy is also expressed in the varying proportion (1/2 to 1/4) of dominant workers (i.e. workers 'above average' in the PCA) in the developmental periods of each colony and between the different colonies. The data indicate that this could be related to the growth rate of the colonies (compare HOGEWEG & HESPER, 1985). Generally, the proportion decreases during colony development, possibly due to an increasing overall dominance of the elite workers. In accordance with this the probability that newly-emerging workers become members of E also decreases during colony development. This view of elite (dominant) workers preventing other workers from becoming dominant, and therefore from laying eggs, is consistent with the observations of RÖSELER (1974) and v. HONK *et al.* (1981). It still remains unclear whether the elite workers, like the queen (v. HONK *et al.*, 1980; RÖSELER *et al.*, 1981), gain their position and inhibit the ascent and the ovarian development of younger workers by means of pheromones as well, or only by means of dominance behaviour.

The position of the queen relative to that of the elite workers also varies from one developmental period to another and from colony to colony. These differences seem to cause differences in the ontogeny of dominance behaviour of the (elite) workers: in colony D the queen had a relatively high position, as in the colony of v. HONK & HOGEWEG (1981), in the first period of colony development, if compared to the position of the queen in colonies A, B and C. (In the first two colonies the elite workers only distinguished themselves from the other workers by a higher activity, in the latter three colonies they also distinguished themselves by a higher dominance index).

The growth rate of each colony is primarily determined by the number of eggs laid by the queen. It seems to be related to the queen's 'switch' to the production of unfertilized eggs ( in fact the 'switch' is a gradual change, lasting 5-6 days, in which the proportion of unfertilized eggs gradually increases), and to the moment at which worker egg laying starts. It is interesting to see that in colonies A, C and D the 'switch' took place 2 weeks before the start of worker egg laying. This has not only consequences for the parentage of the first emerging males, but could also point to a dependence of the start of worker egg laying on the queen's 'switch' (appearance of the first unfertilized, or last fertilized eggs, or simultaneous changes in the pheromonal signals of the queen). However that may be, a relation between the start of worker egg laying and the number of bees in the nest also seems to exist. The queen regularly walks over the comb, contacting every worker she meets; she is the most active bee in the nest but, during colony development, the number of contacts per worker (including elite workers) decreases. Moreover, she seems to reach a maximum level of activity; on the other hand she does not yet give signs of senescence around that time. Therefore we conclude, like v. HONK & HOGEWEG (1981), that force of numbers rather than senescence causes the queen's loss of control. But, as OWEN & PLOWRIGHT (1982) already pointed out, colony size alone cannot explain the beginning of worker egg laying; v. HONK *et al.* (1980, 1981) supposed 70–80 workers was the critical number for *B. terrestris*, whereas in our colonies the workers started ovipositing when they were about 150 in number.

**The Ontogeny of the Laying Worker**

As mentioned earlier a differentiation of elite workers with a higher activity and dominance index than the other workers takes place during colony development. These workers also appear to seek the proximity of the queen more often, and start to buzz there more often than do other workers. Although this retinue and buzzing behaviour is not typical of elite workers, from the frequency with which a worker behaves in these ways it is possible to predict its later position in the hierarchy. As buzzing behaviour is also seen in the colony after disturbance, or if a territory is defended, and furthermore in groups of queenless workers which are establishing a dominance hierarchy (FREE, 1955 ; RÖSELER & RÖSELER, 1977), it clearly has an aggressive character. It is still unknown what the effect of the buzzing behaviour is. Possibly a relation exists between the amount of buzzing near the queen per day and her 'switch' to the production of unfertilized eggs.

Those workers which were (still) members of E in the last period laid eggs. It seems rather contradictory that those workers which had the most contacts with the queen become the egglayers. It is suggested by v. HONK & HOGEWEG (1981) and RÖSELER & v. HONK (1985) that workers which reach a certain stage of ovarian development could become less susceptible to the inhibitory effect of the queen's pheromones and could endure her proximity. This seems improbable since the workers already sought the proximity of the queen from their second day of life onwards. Since, moreover, future elite workers behave in this way more frequently than do other workers, the question arises as to whether the dominance of elite workers is predetermined or the result of the experiences gained in the first day of life. This cannot yet be decided.

Ovarian development appears to be associated with the development of the behaviour patterns associated with egg laying and aggressiveness. These behaviour patterns (except the constructing of egg cells and the eating of eggs) can already be observed a few days before the first worker oviposition. Aggressiveness by workers is shown almost exclusively by a small number of the (future) egglayers, and is directed at most of the egglaying workers (as is the case with the attacks by the queen). Most aggression is seen directly after the start of worker egg laying for a period of about 10 days. This differs from the situation in (artificially composed) queenless colonies, in which the frequency of attacks increased at about the time the first worker laid eggs, but then declined (FREE, 1955). Some workers show behaviour patterns associated with egg laying without really producing an egg. Dissection of such workers shows that some of them could have laid eggs without having been detected, but that the rest had probably stopped their development to egglayers. FREE *et al.* (1969) also found such workers in a colony of *B. lapidarius*.

Like v. HONK *et al.* (1981) we found that the first egglaying workers were among the oldest bees. From then on the number of egglayers rapidly increases. The age at which the young egglayers start to oviposit apparently depends on the growth rate of th olony : 7-8 days in the colonies A, C and D ; 15 days in colony B ; and 24 d in the colony of v. HONK *et al.* (1981). This makes it clear that processes n the individual level are related to processes on the colonial level. In fas owing colonies the development of young workers to egglayers differs only slightly from the development of young workers from queenless groups, which can have ripe eggs from the 5th day onwards (RÖSELER, 1974), but generally oviposit after 6-7 days (own observations). The youngest egglayers had emerged shortly after the start of worker egg laying. Workers emerging around that time have only a small chance of reaching a high position in the hierarchy and laying eggs (*table VI*), probably because of the increasing overall dominance of the elite group. It is interesting to see that nevertheless some workers appear to succeed in 'escaping' from the inhibiting power of the elite group and of the queen, and even develop their ovaries very quickly. The fact that this phenomenon is no longer observed in workers which emerge later suggests that by that time (i.e. during the period of worker egg laying) something has changed.

**The Regulation of the Reproductive Phase**

The queens A, C and D started to produce reproductives (in this case males; new queens are normally reared from the last fertilized eggs) when they had reached the climax of their egg production. Queen B also laid her last fertilized eggs when she was at the climax of her egg production. This had already been observed by CUMBER (1949) and is also suggested by theory (worker-larvae ratio; BRIAN, 1965). These data show that the queen's 'switch' is not linked to a decreasing fertility. It is not known yet which factors indeed cause the 'switch' (POMEROY & PLOWRIGHT, 1982); however, it may be caused by the dynamics of the nest development and social structure (HOGEWEG & HESPER, 1985).

As worker egg laying started 2 weeks after the onset of the queen's 'switch', all first males must be produced by the queen (about 300 in the colonies A, B and D, and probably about 150 in colony C). These data also show that the sex ratio of reproductives produced by the queen would have been male biased. From the start of worker egg laying onwards, egg eating could be observed: the queens of the colonies A, B and D, and to a lesser extent the 'false queen' of colony C, ate most of the workers' eggs, and some of the egglaying workers ate part of the eggs of the (false) queen and of the other egglayers. Therefore, in this period only a few eggs survived and matured, so that we must conclude that the reproductive success of the workers is mostly low and that the queen has the parentage of most of the males. This differs from the findings of v. HONK *et al.* (1981), who estimate that in their colony of *B. terrestris* up to 80 % of the males originate from worker laid eggs. OWEN & PLOWRIGHT (1982) found for *B. melanopygus* that clearly most of the males (61 %) are descended from the queen; the sex ratio of reproductives produced by her is highly male biased. They pointed out that this result is not predicted by kin-selection theory (HAMILTON, 1972; TRIVERS & HARE, 1976). SLADEN (1912, cited in ALFORD, 1975) also reported that 'unless the queen is unprolific or dies early, the workers produce very few offspring, indeed in many nests they produce none!'. On the other hand, KATAYAMA (1971, 1974) found a worker-biased male parentage in one colony each of *B. ignitus* and *B. hypocrita*, and ZUCCHI (1966, in MICHENER, 1974) estimates about 90 % worker-produced males in *B. atratus*. So, apparently, there is great variation among bumblebees. But, in all these species, some males are the descendents of workers, and therefore success in competition among workers for a high dominance rank is ultimately rewarded in terms of fitness.

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