The Ontogeny of the Interaction Structure in Bumble Bee Colonies: A MIRROR Model

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Summary. In this paper we present an individual-oriented model of the behaviour of bumble bees on the comb. We show that the combination of the population dynamics of a bumble bee colony and simple behaviour of the adult bees on the comb is sufficient to generate the social interaction structure of the colony (and its ontogeny) as observed by van Honk and Hogeweg (1981); the latter studied the dominance interactions in a captive *Bombus terrestris* colony in relation to worker oviposition by pattern analysis techniques. We also demonstrate how the generated/observed interaction structure can cause a switch from the production of worker offspring to the production of generative offspring.

The model is an application of the MIRROR modelling strategy (Hogeweg and Hesper 1979, 1981 a, b, c). In this modelling strategy the emphasis is on (i) local definition of entities (individuals), (ii) experience-based interrelations between individuals and (iii) observability. Such models enable us to generate the 'macro' behaviour (in casu of bumble bee colonies) from the 'micro' behaviour (in casu of individual bees) without including (implicitly or explicitly) assumptions about macro relations in the specification of the behaviour of the individuals. Thus the model shows that only those features of the behaviour of the individual bees explicitly incorporated in the model specification are needed to generate the observed organisational pattern in the nest. The model does not, of course, rule out the possibility that other factors play a role in the organisation of live colonies.

social structure, which, being the environment of the individuals, causes a more structured behaviour of the individuals and individual variation in their behaviour.

The case study is based on observations about the interactions between individuals in a bumble bee colony throughout its development (van Honk and Hogeweg 1981). The model presented here, which maps the experience of each, initially identical, individual bee into one continuous variable, is sufficient to produce the observed social structure as reported by van Honk and Hogeweg (1981, p 118), i.e. there are two groups of workers (the 'elite group' and the 'common workers'), distinguished with respect to dominance, interaction frequency and oviposition. Once a worker belongs to the elite she keeps up that status and at the time of her admission to the elite she interacts with the queen and elite workers more frequently than expected. The queen is just as dominant over each worker at the time she leaves the nest as she was before, but because of the size of the nest she can no longer control it.

In fact we studied the simulated nest with identical methods (i.e. pattern analysis of the interactions between individuals) and obtained very similar results. The conclusions referred to above are an interpretation of these results and are therefore just as valid for the simulated nest as for the observed nest. Because the simulated nest is known in yet another way, i.e. by the exhaustive specification of the behaviour of the individual bees, we now know more precisely what is implied by the conclusions drawn from the experimental work.

Introduction

In this paper we present a model for bumble bee colonies as a case study on the interrelations between individual behaviour and social structures. We show how individual behaviour, based on simple rules and using little information, generates a

Materials and Methods

MIRROR Modelling

This study originated from the conjectures that emerged from studying the ontogeny of a captive bumble bee colony by pattern detection methods (van Honk and Hogeweg 1981), and the pattern in colonial development found in that study. The

method used here is 'MIRROR modelling' (Hogeweg and Hesper 1979, 1981a, b, c), followed by the same pattern detection methods as used in the previous publication.

MIRROR modelling consists of a collection of concepts for the heuristic synthesis of certain paradigm systems ('MIRROR worlds'). Unlike models in the strict sense, paradigm systems do not neccessarily represent and simulate empirical entities. Rather, they are defined so as to be paradigmatic for a certain set of relations which are interesting in relation to certain empirical entities and should be known in order to understand the behaviour of these entities (Hogeweg and Hesper 1981c). In our opinion paradigm systems are more useful and, in fact, more abundant in science than the usual simulation models

MIRROR worlds consist of a large number of locally defined entities of different types. Each of these entities has its own properties (variables) and its own behavioral pattern (dependent on its environment). The entities are active 'once in a while' (i.e. it is not so that a fixed set of events happens at fixed time intervals), at which time they interact with their environment changing the values of their own variables and/or those of other entities. The activity of entities can be scheduled in time or is induced by the activity of other entities. Entities are located in spaces and/or they are spaces for other entities. The entities do not interact by a priori defined couplings, but interactions are established dynamically in several ways, e.g. by proximity in some space, by encounters with traces of the other entities, or by memories of previous encounters. (Hogeweg and Hesper 1979, 1981b, c). Therefore entities can be defined independently of the system 'as a whole', which is not the case in more conventional systems-theoretic settings.

A crucial concept in MIRROR modelling is the concept of 'interesting events'. Interesting events are those events that alter some interrelation(s) within the system in such a way that no extrapolation of the state of the entities involved is possible beyond this event unless the event takes place explicitly. Thus, the set of interesting events depends on the set of extrapolation methods available (i.e. the available expectations shaping the model), and may be changed whenever more becomes known about the behaviour of the model (Hogeweg and Hesper 1979, 1981b, c).

MIRSYS, a program written by us in INTERLISP (Teitelman 1974) provides the basic tools for constructing MIRROR worlds. It incorporates tools for the design and creation of entities, for the pseudo-parallel operation of entities, for the scheduling of interesting events in time and the mutual activation of entities (Hogeweg and Hesper 1979, 1981b). Moreover MIRSYS provides for the automatic extrapolation of continuously varying state variables so that they have the correct value whenever they are accessed (i.e. at the time of an interesting event). These (and other) mechanisms are all implemented as locally defined entities similar to those that define a specific MIRROR world.

A full, concise definition of the MIRROR modelling formalism, can be found in Hogeweg (1983), and in previous partial descriptions (Hogeweg and Hesper 1979, 1981a, b, c).

The Model: A MIRROR World for Studying the Social Structure of Bumble Bee Colonies

Introduction

The MIRROR world studied here is designed to represent the ontogeny of a social hierarchy by random ritualised dominance interactions of ini-

tially identical individuals within a population dynamic setting comparable to bumble bee colonies. All differences between individuals are caused by these interactions, and the experience of an animal is mapped into one variable.

It should be stressed that the behaviour pattern has been made up in order to define a simple bee-like animal with regard to which the concept 'social structure' would make sense, and whose behaviour would be constrained in a local way by external factors (availability of food, time, etc.). Nevertheless, for those behaviour elements for which we could use the available knowledge about bumble bees as well as some arbitrary construction, we chose the former. However, lacking details needed to derive a sufficient description of our bee-like animals were simply 'made up' (see Table 1). On the other hand, many theories about the regulation of the behaviour of bumble bees were not used in the model since they proved to be superfluous for generating the desired behaviour.

The individual bees are the basic entities in the MIRROR world. They are defined in terms of possible ways in which they interact with their environment; they are active once in a while and produce the 'interesting events' of the world. The interesting events in this MIRROR world are in the first place the interactions between bees, because these interactions change the expectations about the future behaviour of the individual. Other interesting events are population dynamic events (oviposition, hatching of eggs, pupation, eclosion, death) and 'maintenance' events (feeding itself, feeding larvae, foraging). The maintenance events are included to reflect the viability of the world and because they play a role in interfacing the population dynamics and the social interactions.

It is, of course, not feasible to let the model entities interact as frequently as live bees do because of the need for excessive computer time (i.e. an amount of computer time equal or exceeding the duration of the development of live nests). Therefore the activity of the MIRROR bees amounts to only about 10 actions a 'day' (for $D = 1$ as in newly hatched bees, see Table 1), where days are identified in relation to the population dynamic parameters. This activity is, of course, far less than the activity of live bumble bees: the half-hour observations of interaction among the bees on a comb indicate 5–10 dominance interactions per hour for average workers; the feeding data of Pendrel and Plowright (1981) indicate 5–10 such feeding interactions per hour for the one worker studied. Thus one activity in the MIRROR world stands for a number of actions, e.g. for an activity

Table 1. Parameters of the MIRROR bumble bee nests (compare text) Values of example of Results. *1* Röseler (1970) gives these values for *Bombus terrestris*; *2* Michener (1974) reports overlap of generations in field-nests, but less variation in captive nests; *3* van Honk (personal communication) reports 2–3 cells/pupa; overall growthrate matches captive nest (van Honk and Hogeweg 1981); *4* arbitrary constant, scaled to match ACT; *5, 6* arbitrary constants, scaled relative to each other

Parameter	Value	Interpretation	Notes
Population dynamic parameters			
EGGDT	4 days	Egg development time	(1)
VEGGDT	1 day	Standard deviation of EGGDT	(2)
LARVDT	7 days	Larva development time	(1)
VLARVDT	2 days	Standard deviation of LARVDT	(2)
QLARVDT	3 days	Extra development time for new queens	(1)
PRESSDT	4 days	Period that queen-rearing can be suppressed	(1)
PUPDT	10 days	Pupa development time	(1)
VPUPDT	2 days	Standard deviation of PUPDT	(2)
PUPEGGDT	3 days	Period that pupae are suitable for oviposition	(1)
FIRSTBR	5 workers	Number of workers initially laid by queen	(1)
POVI	0.6	Probability that a pupa is full after laying of egg	(3)
OVIT	0.04 days	Duration of oviposition	(4)
BOVIT	0.15 days	Duration of cell building	(4)
PEAT	1	Probability of eating eggs	(arbitrary)
Maintenance parameters			
IHONEY	10	Amount of honey initially in *pot*	(5)
MBITE	1	Maximum amount of honey taken from *pot*	(5) Eq. 4
DIGEST	0.2/day	Amount of food digested per day	(4)
LBITE	0.2	Amount of food transferred to larva per feeding	(4)
QLBITE	0.3	Amount of food transferred to new queen larva	(5)
QRAISE	5.5	Min amount of food in larva for raising a new queen	(5)
EATT	0.2 days	Amount of time spent at *pot*	(4)
CATCH	2	Amount of honey brought to *pot* by forager	(5)
CATCHT	0.3 days	Amount of time that forager spends in *outside*	(4)
Dominance parameters			
IQDOM	7.5	Initial value of D of queen	(6)
IWDOM	1	Initial value of D of worker	(6)
STPDOM	0.15	Parameter for updating D variables	(4) Eq. 2
INCEN	0.15	Parameter for time spent in *center*	(4)
STRESSM	1	Stress-threshold for laying of drones (per oviposition)	(4)
STRESSK	3	Stress-threshold for killing of queen (per oviposition)	(4)
Activity parameter			
ACT	0.1	Parameter for waiting time in between activation	cf. (4) Eq. 1

bout as observed by Pendrel and Plowright (1981) and Oster (1976), but, contrary to such activity bouts, involves only one interaction partner. Experiments with alternative MIRROR worlds, in which the activity of all members of the nest is doubled or halved, and in which the effect of the activity is changed accordingly (e.g. feeding, eating etc. half the amount, and updating the D variable by half as much when activity is doubled) indicate that the structure of the nest is not affected by these changes.

The colony was observed by recording interactions between adult bees in the same manner as for an experimentally grown bumble bee colony by van Honk and Hogeweg (1981), and by record-

ing worker ovipositions. These data allow identical processing of the data of the MIRROR world and the experimental data.

The MIRROR world was also observed in several other ways:

(1) periodically the number of individuals in each region of state-space and of nest space were counted;

(2) a complete protocol of the behaviour of some individuals was recorded;

(3) a complete inventory of certain types of events (e.g. all killings of eggs, all feedings of larvae, etc) was made;

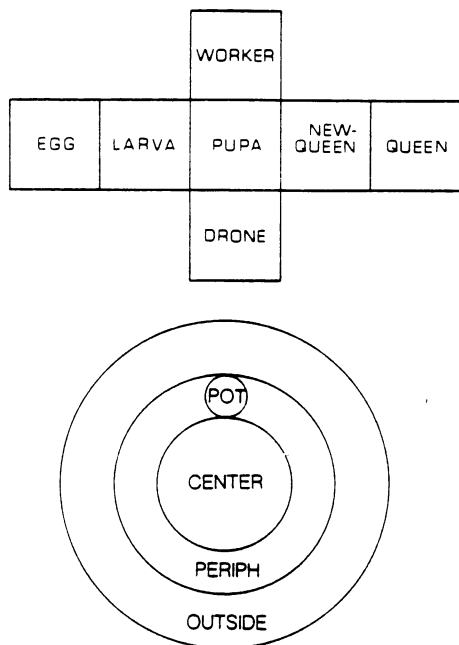(4) the history of values of certain properties of each individual was recorded.

Fig. 1. Configuration of the spaces. *Above* patches of the state-space (developmental stages); *Below* patches of the nest-space (Comb)

Specification of the Model

Notational convention: following common practice we assign mnemonic names to the model entities (e.g. QUEEN, WORKER) and write these in capitals to distinguish them unequivocally from entities in the empirical world (e.g. queen, worker).

The entities for implementing the particular world studied here are, in the first place; BUMBLEs. There are two spaces defined, the state-space and the nest-space (COMB). The state-space is subdivided into six regions: *egg, larva, pupa, worker, drone, newqueen* and *queen*, connected as shown in Fig. 1. In the experiments described here the region *queen* was occupied from the start by only one BUMBLE, the other BUMBLEs moved through the other regions of this space scheduling the interesting event of their passing into the next region at the appropriate time (moving rates, which represent duration of developmental stages, are given in Table 1). At intermediate times the exact position of a BUMBLE in the region was calculated only when another BUMBLE requested this information. For example the location of a BUMBLE in *pupa* could be requested by the ·BUMBLE in *queen* or by BUMBLEs in *worker* to find out whether it was in good condition to serve as location for a new BUMBLE in *egg*. (Hereafter we will shorten ·BUMBLE in *queen* ' to QUEEN, etc.).

The BUMBLEs also move about in the ·nest-space': It consists of the regions: *center, periph, pot* and *outside* connected as shown in Fig. 1. *Center* is defined as the part of the nest-space where the QUEEN and the brood are, and where the interactions between the animals take place and are recorded (in live nests this region may be located in the periphery). *Periph* represents the remainder of the nest where no activities take place (i.e. are recorded), *pot* represents the honey pot, and *outside* is the foraging area.

Each BUMBLE has a variable, D: when BUMBLEs become WORKERs it is set to a value identical for all WORKERs (parameter: IWDOM), while for the QUEEN it is set to another value (parameter: IQDOM). This D variable, and its changes, regulates many actions of the BUMBLEs; it is updated by the action DODOM (see Ritualised dominance behaviour).

The QUEEN and the WORKERs are activated periodically. The waiting time between activations depends on the D variable:

$$WT := ACT/D \tag{1}$$

where WT is the time between activations, ACT is the overall activity parameter and D is the D variable of the BUMBLE under consideration. Van Honk and Hogeweg (1981) found a correlation between dominance and activity.

At each activation they select at random an interaction partner in the region of the nest-space in which they are located (here always *center*). Their subsequent behaviour pattern depends on the location of the interaction partner in state-space as described below.

Ritualised Dominance Behaviour

If the interaction partner is a WORKER or QUEEN, the active BUMBLE performs the action DODOM, which in the model gives rise to an interaction comparable to the dominance interaction as recognised by van Honk (1981) in live bumble bee colonies: two bees meeting each other antennate, and one gives way to the other.

The occurrences of DODOM are the most crucial events in this MIRROR world: the one memory variable is updated and the principal observations on the colony consist of the recording of such events. DODOM represents what can be called a 'ritualised dominance' interaction: when the outcome of the interaction (i.e. who gives way to whom) reflects established dominance relations, these are slightly reinforced by the event, but when the outcome is counter to the established dominance, there is a much more pronounced change

in the dominance variables of the interacting BUMBLEs. DODOM is algorithmically defined as:

$$R := D_M/(D_Y + D_M)$$

if RAND(R) then $K := 1$ else $K := 0$ (2)

$$D_M := D_M + (K-R)*STPDOM$$

$$D_Y := D_Y - (K-R)*STPDOM$$

where D_M and D_Y are the dominance variables of the active BUMBLE and of its interaction partner respectively. R is the dominance index as defined in van Honk and Hogeweg (1981), and RAND represents a random drawing from a uniform distribution between 0 and 1, whose value is 'true' if R > random value and 'false' otherwise; STPDOM is a scaling parameter.

Thus, if $D_M \gg D_Y$ then K is almost always 1 and D_M is slightly increased by the interaction, whereas D_Y is slightly decreased by the interaction. However, when K happens to be 0, D_M is sharply decreased and D_Y sharply increased by the interaction. On average, increase and decrease are equal for a certain value of R. However, because the D_M of a BUMBLE changes, the average R of a BUMBLE towards the other BUMBLEs in the nest changes. By this mechanism a differentiation between initially identical BUMBLEs can be established, as shown below.

Feeding of the LARVAe and Rearing of NEWQUEENs

If the interaction partner is a LARVA, a WORKER will feed it (i.e. an amount of food (parameter: LBITE) is transferred from the WORKER to the LARVA). When the LARVA has accumulated food above a certain threshold value (parameter: QRAISE), it is reared henceforward as a NEWQUEEN: it is given more food per feeding (parameter: QLBITE) and its development time is increased (parameter: QLARVDT).

The QUEEN only feeds LARVAe in the initial stages of the nest development: the probability of her feeding a LARVA which she has encountered decreases reciprocally with her age. When the QUEEN encounters a LARVA which is being reared as a NEWQUEEN she will inhibit its development into a QUEEN (parameter: PRESSDT) (Röseler 1970, demonstrated this effect for *Bombus terrestris*, and its absence in *Bombus hypnorum*).

Oviposition and Stress of the QUEEN

If the interaction partner is a PUPA, and the PUPA is young enough (parameter: PU-

PEGGDT), an 'egg cell' (CELL) is built on top of it. Either the QUEEN or WORKERs build these CELLs. The CELLs built by the QUEEN are used by herself for ovipositions. The QUEEN will also use the CELLs built by the WORKERs if she has time to do so (not busy elsewhere in the nest) and if the WORKER has not abandoned the CELL before finishing it, which happens if her D variable has decreased during the building of the CELL. If the QUEEN does not use the CELL, the WORKER who has built the CELL will do so if and only if her D variable has increased during the building period (parameter: BOVIT).

During oviposition of the QUEEN (which takes time, parameter: OVIT) DODOM interactions with WORKERs, and in particular those not 'won' by the QUEEN, increase her 'stress' (each DODOM adds one to stress; while for each DODOM lost one more is added). If, during an oviposition, the stress reaches a threshold value (parameter: STRESSM), the QUEEN produces unfertilised (drone) EGGs; otherwise she produces fertilised (worker) EGGs. WORKERs always produce unfertilised EGGs and need to have won an interaction during the building period to do this. The stress parameter of the QUEEN is used for yet another purpose: if it reaches an even higher threshold (parameter: STRESSK), the QUEEN leaves the comb and eventually dies.

PUPAe are pushed into *periph* when they are entirely covered with occupied egg cells (parameter: POVI) and are henceforward no longer available as interaction partners.

Eating of EGGs

If the interaction partner is an EGG, an ovipositing BUMBLE (QUEEN or WORKER) might eat it if it is not her own. The probability of eating the EGG is a constant (parameter: PEAT), but the probability of encountering an EGG, of course, is not.

Eating and Foraging

Eating and foraging activities occur independently of the activity cycle described above. Each BUMBLE has a continuous variable: FOOD. Food is supposed to be digested at a constant rate (parameter: DIGEST). The variable FOOD is updated accordingly whenever its value is used by some entity in the system, e.g. when the LARVAe are being fed and food is being transferred. Furthermore, when all food has been digested the BUMBLE receives a hunger signal which causes her to move to *pot*, to eat (if enough honey is

available) and return. If, however the honey is low relative to her norm, she will go *outside* to forage, return to replenish *pot*, eat and return to *center* or *periph* (parameters: EATT, CATCHT, CATCH). The norm which causes foraging behaviour is again dependent on the D variable:

$$H < = 1/D_M + BITE \qquad (3)$$

where H is the amount of honey, and BITE is the amount she will eat. Thus, the BUMBLEs with lower D values are more prone to foraging when they go to *pot*. Moreover the amount eaten per visit to *pot* also depends on D:

$$BITE := MIN(D_M, 1) * MBITE \qquad (4)$$

where MBITE is a parameter giving the maximum food intake. Thus, the less active BUMBLEs eat less at a time than active BUMBLEs; the active BUMBLEs use more food to feed the LARVAe.

Movements in Nest-Space

Apart from movements in relation to eating and foraging, the BUMBLEs move between *center* and *periph*. Between activations a BUMBLE spends part of its time in *center* (maximally parameter: INCEN) and the remaining time in *periph*. Thus, when she has high activity, she remains in *center*, otherwise she spends some time in *periph* after an activation. While a BUMBLE is in *center*, she is supposed to be busy on the nest and she can be chosen as an interaction partner by other bees, whereas while she is in *periph* she is supposed to be resting in a quiet corner and will in that case not be chosen as an interaction partner by other BUMBLEs. In this way the interaction frequency between any two BUMBLEs depends on the product of the activities of both, which is in accordance with the findings of van Honk and Hogeweg (1981).

Initiation of the Nest

The QUEEN initiates the nest by generating a number of BUMBLEs (parameter: FIRSTBR) in *egg* before she enters the activity cycle described above.

Ontogeny of the BUMBLEs

BUMBLEs start life as EGGs, i.e. in the egg region of the state-space, and move through state-space as they develop into LARVAe, PUPAe, WORKERs, DRONEs or NEWQUEENs. It is only transitions from one state to the next which happen explicitly in the model, because these events change the behaviour of the BUMBLEs. In the model the rate of development is independent of other processes: in particular no account is taken of the amount of food given to the LARVAe. This is contrary to the findings of Plowright and Pondrel (1977) who found that development rate depends on food intake and that development can be delayed arbitrarily. For simplicity these findings are not incorporated in the model: instead average development times are taken from the literature (see Table 1) and the development rate of an individual is chosen randomly from these average values.

'Time Spent' Mechanism

The activities of eating, foraging and oviposition take time (see Table 1), and during such periods no other activities take place. The building of CELLs also takes time but during such periods normal activities take place, although not more than one CELL is built at a time. This 'time spent' mechanism, together with the random choice interaction partners interfaces the behaviour of the bees with the population dynamics of the nest.

Summary of the Model

The model bumble bees develop from eggs into one of the adult states in approximately the time required for live bumble bees, they are fed during the larval stage and serve as site for oviposition at their pupal stage. They start their adult life in an identical state (differences in the amount they are fed are not used). In the adult stage they interact randomly with the members of the nest in the region in which they find themselves. Interactions with other adults are ritualised dominance interactions by which one memory variable is updated. Other activities of the adults are: feeding themselves and the larvae, foraging, building nest cells and ovipositing.

The full specification of the MIRROR world has now been given. All relations mentioned hereafter are results that follow from the above defined behaviour of the individuals and are not additional assumptions.

Results

The Behaviour of a MIRROR Bumble Bee Comb

In this section we describe an example of a MIRROR bumble bee comb, which is representative for about 20 similar simulated nests. The values of the parameters are given in Table 1. Fig-
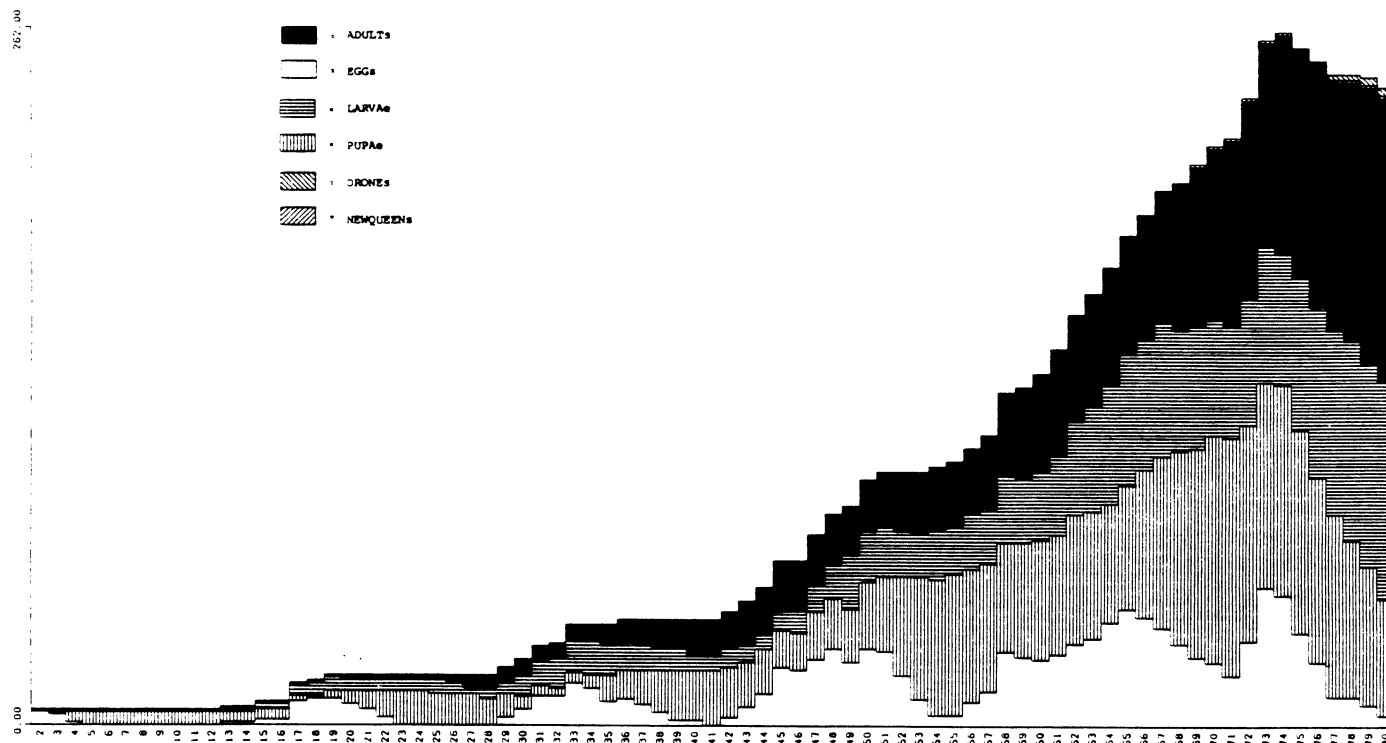
Fig. 2. Nest composition and development. *Horizontal axis:* time in days; *vertical axis:* number of entities in the various developmental stages (Adults = Workers + Queen)

ure 2 shows the population development of the nest subdivided into members of the different developmental states: EGGs, LARVAe, PUPAe, WORKERs, NEWQUEENs, and DRONEs. It also shows that the growth pattern of the nest is irregular in the sense that sudden increases occur in the number of nest members in the different states, in particular at the beginning of the nest development. Of course, the ratio of the number of animals in the different states changes as well. The irregularities in the pattern are, obviously, caused by the time-lag in the development and the exploitation of the (young) PUPAe as sites for oviposition; the temporal differentiation in behaviour and resources which these mechanisms produce, generates many of the properties of the social structure of the nest.

Inspection of the protocols of the behaviour of various animals shows clearly the temporal and individual differentiation in their behaviour: e.g. the QUEEN spends her time mainly interacting with WORKERs, and in certain periods she lays eggs (PUPAe have become available for this purpose). Elite WORKERs (this classification is obtained below), being less active than the QUEEN, but much more active then the common WORKERs, are very busy feeding the LARVAe

and, to a lesser extent, interacting with WORKERs; for the latter interactions the elite WORKER is most often the one who takes the initiative. The common WORKER is chosen relatively frequently as an interaction partner (and therefore interacts more often with elite WORKERs than with other common WORKERs); when hungry, the common WORKER is likely to go out foraging; she does so more frequently than more active elite WORKERs (thus active means active on the comb, not necessarily off the comb).

The QUEEN is pushed off the comb shortly after the first WORKER has laid an EGG and the QUEEN has laid some drone EGGs. Soon after the QUEEN has left the comb many workers start to lay EGGs and to eat the EGGs of the QUEEN and of other WORKERs. This causes a rapid decrease in the number of EGGs and, somewhat later, in the number of LARVAe. The adult/larva ratio increases and many of the LARVAe of the QUEEN are reared as NEWQUEENs, whereas previously this happened rarely. Thus the colony starts to produce mainly generative offspring, whereas before it produced mainly worker offspring. Thus the social forces caused by the individual behaviour cause the switch-over to genera-

tive offspring production, which is recognised as being energetically optimal in the context of optimality studies (e.g. Brian 1968; Oster and Wilson 1978).

The D variable of the BUMBLEs, which is set to 1 just after eclosion in all BUMBLEs, shows a differentiation. Although the values of D do not show a gap in their distribution and although the D of each bee fluctuates, the differentiation is of a permanent character: once the D of a BUMBLE is well above average, it will remain above average. The D of the QUEEN also fluctuates but remains around the initial value throughout the development of the colony: even at the end of the colony, when the BUMBLEs start laying EGGs, and when the QUEEN is pushed off the comb, her D value is around initial value, and the values of the Ds of the BUMBLEs are far less. Thus it is not a relative decrease in the D variable which causes the QUEENs loss of dominance. This is in accordance with experimental findings for live bumble bee colonies where the queen in this phase is as able as ever to organise the nest structure when she is moved to assembly of young bees without a queen.

However, the D variable is not an observable feature of live bumble bees and should therefore not be used to judge the social relationships in the colony. Therefore, we observed these social relationships in exactly the same way as by van Honk and Hogeweg (1981). The data on the encounters between adult BUMBLEs in *center* were recorded: for each interaction between adult BUMBLEs it is scored who gives way to whom. These data are lumped into an asymmetrical interaction matrix for each stage in the nest development. This interaction matrix serves as a basis for calculating the social similarity between the BUMBLEs: two BUMBLEs are similar when they interact similarly with all other bees (van Honk and Hogeweg 1981). The social structure of the nest is then represented with the help of principal coordinate analysis (Gower 1966) or cluster analysis— the former produces an ordering of the individuals along one axis, and the latter generates groups of similar individuals. The result of the pattern analysis as depicted in Figs. 3 and 4 shows that:

1. There are two groups of WORKERs, which can be called the 'elite' and the 'common workers'. The elite is on the QUEEN's side of the axis found by principal coordinate analysis, and is joined to the QUEEN at a higher similarity level than the common workers.

2. The elite can be distinguished by its higher frequency of interactions with the QUEEN and

some WORKERs: some of the latter are in the elite and others in the common worker cluster; they seem to be the WORKERs who are trying to or have just succeeded in entering the elite.

3. Once a WORKER has entered the elite she usually remains there, although there are a few WORKERs who 'digress' into common workers (here only no. 24), after spending a period in the elite.

4. The elite WORKERs lay EGGs (each oviposition is indicated by an asterisk in Figs. 3, 4).

5. After the QUEEN has been pushed off the comb 'chaos breaks loose' (see Figs. 3, 4); several elite WORKERs drop down to the common worker side of the principal axis and many new elite WORKERs emerge. The results of the cluster analysis and principal component analysis are far less in agreement than before, indicating less clearly defined hierarchy and grouping.

6. The dominance of the QUEEN as seen in the PCA and cluster analysis remains constant during all stages in which she is present.

This pattern is very similar to the one observed in the live bumble bee colony. We can therefore conclude that the very local information on the basis of which the behaviour of our MIRROR bumble bees is defined is sufficient to generate the pattern of behaviour of the comb. In particular we see that:

1. No initial differences in the workers are needed to generate the observed differences in their later behaviour (in particular oviposition).

2. The behavioural differentiation can be caused entirely by chance meetings.

3. No global factors influencing the bees are needed to display the observed behaviour. In particular a bee does not have to be aware of the queen and her dominance 'all the time'; her chance meetings with the queen and other bees (who meet the queen also) are sufficient to let the queen 'organise' the nest.

4. The oviposition of the workers may depend on increase in dominance rather than on the absolute value of the D variable: this is likely to stabilise the behaviour of the nest because the workers with the highest D variable will be likely to lay EGGs irrespective of the absolute value of the D.

5. The MIRROR bumble bee colonies reveal an interesting relation between the production of DRONEs and NEWQUEENs. The production of queen-DRONEs depends on the difference between the two stress thresholds: if DRONEs are produced at much lower stress values than those that drive the QUEEN off the nest, the QUEEN will produce mainly (only) DRONEs in the latter
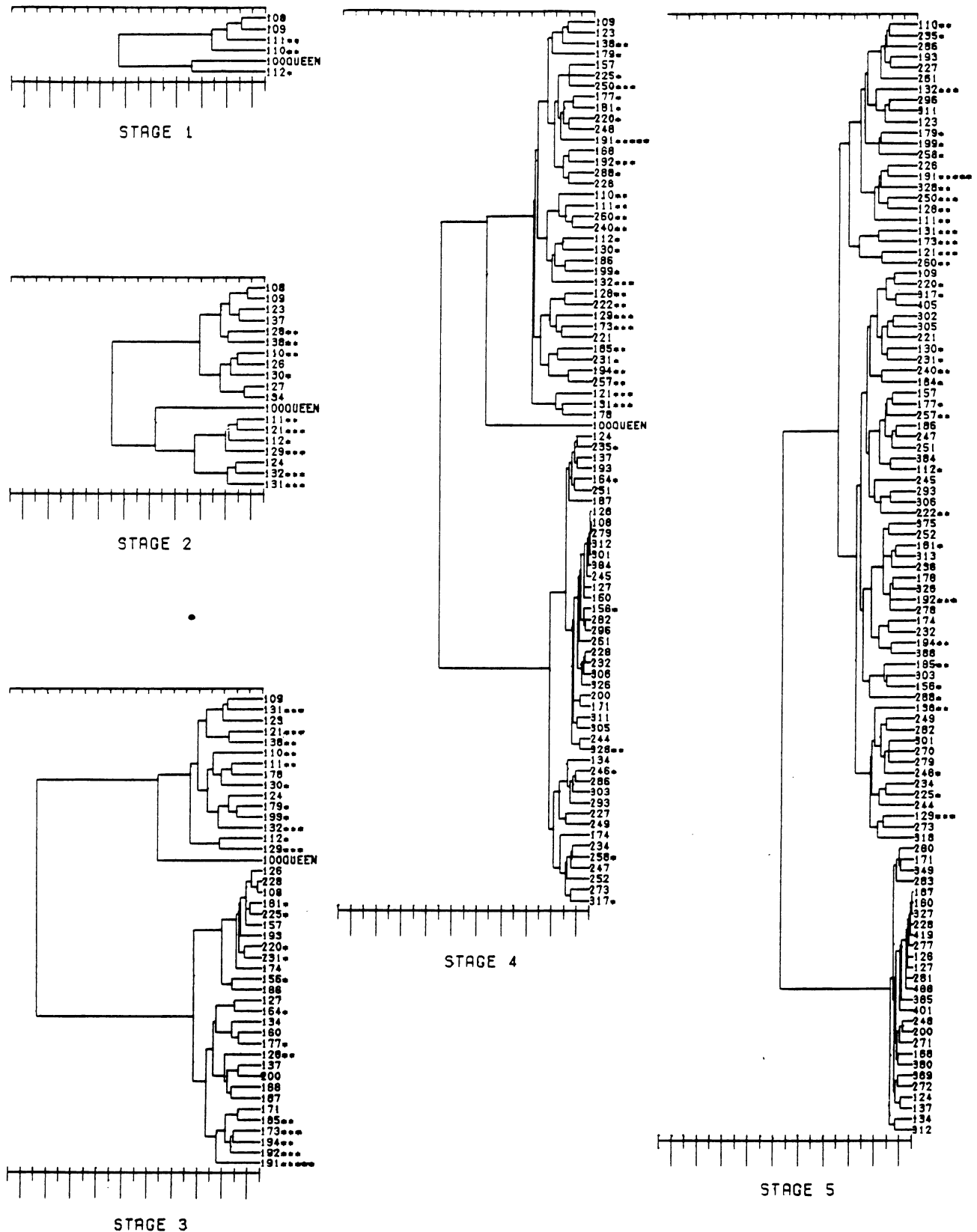
Fig. 3. Dendrograms of the similarity of the adult bees (Workers and Queen) at each stage of nest development. The numbers which identify the bees are ranked according to the age of the bees but are not consecutive (other entities of the MIRROR world used the missing numbers). Oviposition of the workers is indicated by an asterisk; in stage 5 all ovipositions occurred after the Queen had left. After 80 'days' the nest was terminated. Cluster criterium: mean city block distances, Ward averages. Data: Number of DODOM interactions of each of the bees with each of the other bees and dominance index of each of the bees with each of the other bees (cf. similarity criterion 6 in van Honk and Hogeweg 1981)
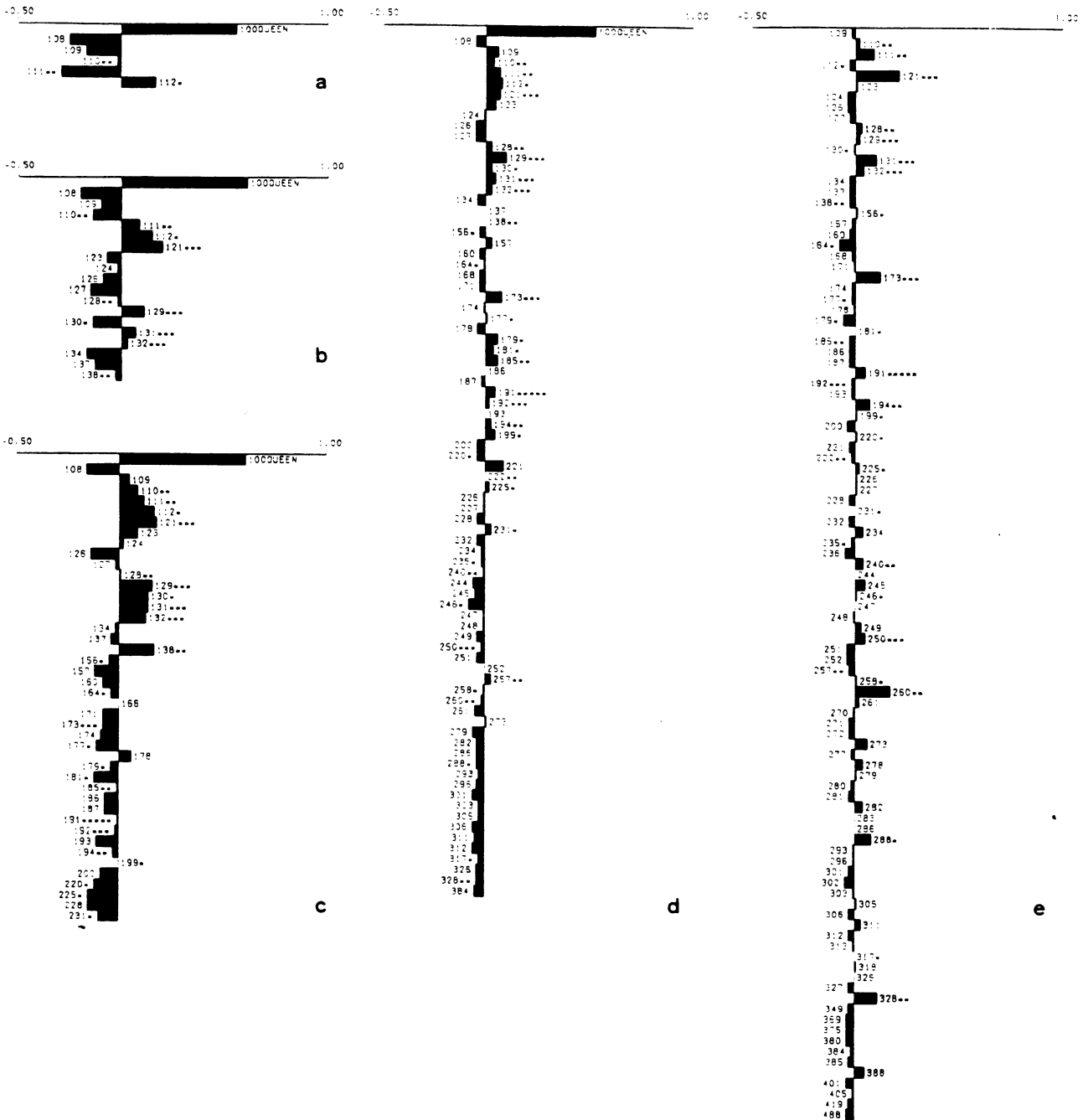
Fig. 4a–e. First principal coordinate axis of the similarity between the adult bees at each stage of nest development. *Vertical axis:* bees ordered according to age. *Horizontal axis:* value on principal coordinate. See further caption to Fig. 3

stages of the nest. If this is the case, then the increase in the ADULT LARVA ratio caused by the eating of eggs after the QUEEN has been pushed off will not produce NEWQUEENs because no more female larvae will be available. If the QUEEN produces fertilised EGGs up to a very

short time before her departure, the ratio of DRONEs vs NEWQUEENs will depend on the severity of egg predation. Thus it seems that in the latter case the ratio will be determined not by a 'queen-worker' conflict (Trivers and Hare 1976) but by a 'worker-worker' conflict!

Comparisons Between MIRROR Worlds with Different Parameter Values

So far no exhaustive study of all possible combinations of parameter values has been undertaken: too few experimental data are available to evaluate such a study. In this section we pay attention, however, to some features of the various MIRROR worlds which we did study; the features could serve as guidelines for further research.

In particular we shall discuss (1) the factors responsible for the generation of the elite, (2) the effect of altering the growth rate of the nest, (3) features of the switch.

Generation of the Elite

Both the observed live nest and the presented MIRROR world showed that an elite group gradually established itself. It consisted mainly of somewhat older workers, but the age of entry to the elite varied greatly. Once an insect had entered the elite, she remained there and only very few regressed into the common worker group before the last stage of the nest, when chaos reigns. This consistency of the elite group depends critically on who meets whom, i.e. on the fact that less active (and therefore also less dominant) bees spend a considerable time in *periph* and during that time are not chosen as interaction partners. Therefore, the chance of bees meeting depends on the product of the activity of the two bees, as was observed in the live colony. Thus, in addition to the local interactions of pairs of bees, there is one global factor, the spatial differentiation of the nest in *center* and *periph*. If the time spent in *center* (parameter: INCEN) is too long (i.e. there his little spatial differentiation between active and less active bees) the consistency of the elite disintegrates: although at any one time there are the clearly defined groups of the elite and the common workers, regression of elite WORKERs to common WORKERs occurs quite frequently. Alternatively, if the WORKERs spend very little time in *center*, they interact very infrequently with each other and the two-group structure becomes less clear and subgroups emerge.

In this context it should be mentioned that it is also crucial for the observed social structure that the dominance of an animal and its activity be directly related, in the sense that the more active animals are the more dominant ones, although the exact form of this relation may be less crucial. Note that in the pattern analysis both activity and dominance were used as features, but that the use of

either feature produced similar results in the live nest (van Honk and Hogeweg 1981).

Growth Rate of the Nest

The generation of the social structure depends on the population dynamic features of the nest. If the growth rate is too high, the workers are so busy feeding the larvae that they interact only infrequently with each other and a less well-defined group structure results. Owing to the sudden addition of many new workers to the nest (which initially have an intermediate dominance i.e. for which the ritualised dominance is less ritualised) many regressions from the elite group to the common group occur. Preliminary observations on a fast growing, live bumble bee colony showed a similar decrease in the consistency of the groups (van Doorn et al., in preparation). If the growth rate of the nest is too slow, one or a few workers will often attain very high dominance and come to the level of the queen long before the switch is due (at the time of the switch the queen still holds her high dominance in a normal nest).

The Switch from Worker to Generative Offspring

The switch from the reproduction of worker offspring to the production of generative offspring occurs in the present setting without external influences (e.g. food availability) as a purely population dynamic feature; likewise the switch occurs in captive colonies although they are fed at a constant rate. It has been pointed out (Oster and Wilson 1978) that to generate mature generative offspring the colony has to start laying the appropriate eggs and rearing new queens several weeks before the 'end of the season', when apparently conditions become less favorable; however, in these last weeks sufficient food has to be available. Therefore an external (e.g. food) signal should be of a qualitative rather than a quantitative nature. A possible alternative for such a difficult qualitative external signal is an internal, population dynamic, 'signal', which can evolve to match prevailing external conditions. Such an internal signal should be relatively stable with regard to fluctuating external conditions, e.g. it should occur around the same time, independent of the precise growth rate of the nest and independent of the fate of the workers.

In the present setting the switch is caused by two different mechanisms: the stress of the QUEEN, which depends on the number of her interactions with the WORKERs, the dominance ratio of the QUEEN and the WORKERs, and the

lack of time to use all the CELLs built. Together these mechanisms favour the desired stability of the switch: in slow growing nests, the WORKERs are not very busy feeding the LARVAe and they interact relatively frequently with each other and with the QUEEN. In such nests some WORKERs tend to obtain high D values. Because of the frequent interactions and the high D values the stress of the QUEEN will reach its threshold value although the nest is relatively small. In fast growing nests the QUEEN will spend more time ovipositing, and therefore less frequent interaction can still increase the stress of the QUEEN to such an extent that she is pushed off the nest. However, it is more probable that the QUEEN becomes too busy to oviposit in all the CELLs built and the WORKERs will start to oviposit. Ovipositing WORKERs will henceforward defend their own CELLs and fewer CELLs will become available for the QUEEN. Ovipositing WORKERs will, moreover, eat EGGs, thus reducing the population growth. Therefore, in such nests the QUEEN may remain on the nest but nevertheless lose control.

Discussion

Ritualised Dominance Behaviour

The ritualised dominance interaction incorporates an interesting, counter-intuitive feature, a version of which was in fact observed in the live nest. Although interaction with an individual higher in the social hierarchy will usually lead to a decline in the social position of the lower placed animal, such interactions are ultimately the best way to ascend in the dominance hierarchy: it is only interactions of this kind which can cause appreciable increase in dominance. Analogously, in the live nest, although the queen inhibits ovary development in the workers (Röseler 1974; van Honk et al. 1980; Röseler et al. 1981), the workers that had more frequent interaction with the queen are the ones to lay eggs in the last stages of the nest.

Ritualised dominance is defined here in an informational sense. Speculations about its physical implementation in bumble bees or in other species are left to experts on these species.

'Random' Interactions

The model bumble bees meet at random other members of the (part of the) nest in which they find themselves. This feature was originally chosen because it seemed the most simple assumption. Given this assumption, differentiation of the nest in two regions was essential in producing the pattern of colony development. It is very interesting to compare this with the experimental results of Seeley (1982) on honey bee colonies: developmental castes in bee colonies perform a set of tasks and a switch occurs from one set of tasks to another. Seeley showed that the various sets of tasks are the ones to be performed in certain regions of the nest. Thus it seems that the differentiation in regions is stronger and more varied in the larger bee colonies, but that the bees, like our model bumble bees, chose their tasks from what is to be done. In such a different environment ritualised dominance is likely to give rise to different development of the nest, possibly to that observed in honey bees!

Identical Newly Hatched Workers

The model workers start their adult live in a blank state identical for all workers. They are, however, not all fed the same amount, which would presumably lead to initial but immutable size differences. Such size differences correlate with dominance in experimental situations in which a set of workers of identical age interact (Röseler and Röseler 1977; van Doorn and Hogeweg 1982). Size is not the determining factor for dominance in undisturbed captive nest, in which case dominance and oviposition do not correlate with size (van Honk 1981; van Doorn and Hogeweg 1982). This fact and the results of the present study that the effect of ritualised dominance behaviour depends crucially on nest composition indicates that data on social interactions of artifical assemblies of bees can be very misleading.

Conclusions

Dominance structure as observed in bumble bee colonies can be generated by ritualised dominance behaviour of initially identical worker bees and a queen who meet by chance on the comb. The ritualised dominance behaviour adjusts the dominance variable of the individuals in such a way that when established dominance relations prevail, the chance meeting only slightly changes the dominance relations, whereas when a chance meeting results in the less dominant animal dominating the more dominant one (as measured by the D variable) the dominance relations are greatly affected. The social position of the winning bee is then sharply increased and that of the loosing bee sharply decreased. Interaction between bees with similar dominance are less 'ritualised' then those

between dissimilar bees: increase and decrease are moderate and depend only on who wins. The ritualised dominance behaviour generates a stable elite group only if it occurs in the appropriate setting, i.e. in a nest in which a spatial differentiation is maintained between the center and the periphery, and in which the population dynamics resembles the one of bumble bee colonies.

The generated social structure, the population dynamics, and the stress of the queen cause a switch from the production of worker offspring to the production of generative offspring; such a switch has been recognised as optimal in the context of optimality studies. The mechanism that causes the switch in the MIRROR world can evolve to match prevailing environmental conditions (e.g. climatic conditions) and is fairly unaffected by chance fluctuations in nest development. However, as in live nests, there is much variation in several features of the switch: the queen may or may not be pushed off the comb, the ratio of worker-drones vs queen-drones and of drones vs new queens is strongly influenced by minimal changes in the parameters.

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