Socioinformatic Processes: MIRROR Modelling Methodology

P. Hogeweg and B. Hesper

Bioinformatica, Padualaan 8, Utrecht, the Netherlands

Socioinformatic processes are defined here as informatic processes which cause behavioural differentiation among individuals who are basically equal, thus generating a social structure in groups of individuals.

We discuss a formalism in which such socioinformatic processes can be modelled in a natural way, using concepts of MIRROR modelling (Hogeweg & Hesper, 1979, 1981 a,b,c; Hogeweg, 1984).

We present two very simple principles for the behaviour of individuals and show these to be sufficient to generate "interesting" social structures.

Interesting because the generated social structure depends on other, non-social properties of the animals under consideration (e.g. population dynamic and ontogenetic properties). As an example we show that the thus generated social structure coincides with the social structure of bumble bee colonies if and only if applied in the context of the population dynamics of bumble bee colonies. We discuss how in other contexts (and if somewhat differently implemented) these principles might generate the social structure of groups of other animals, e.g. monkeys.

Interesting, moreover, because the generated social structures are self-regulating and relatively resistant to variation in behavioural traits related to the socioinformatic processes, although a social structure tends to change drastically when in a different environmental context (e.g. under the influence of a change in population dynamic parameters).

Finally we discuss the impact of such socioinformatic processes on the evolution of behavioural traits in individuals, and compare our findings with modelling strategies currently used in the study of behaviour patterns.

1. Introduction

In this paper we discuss socioinformatic processes as a special (simple) case of processes generated by the interaction between independently defined spatio-temporal entities (henceforward called "individuals").

Socioinformatic processes differ from e.g. ecoinformatic processes in that the individuals are "equal" in the sense that they can receive/convey similar (in some well-defined sense) information and use identical encoding/decoding processes in the interpretation of this information. Socioinformatic processes occur in groups of equal individuals and according to our definition cause differentiation of the behaviour of the individuals.

If and only if the individuals do indeed exist separately and not as "parts of a whole", "social structure" is an emergent property of the system and is not a hidden input parameter; it is generated non-trivially by the individuals in that it is generated from their behavioural definition, (which is not in terms of social structures) in relation to the environment in which they find themselves.

Thus, in studying socioinformatic processes one needs a modelling formalism which allows individuals to have a separate existence. Such a formalism is described in section 2. Experimenting with this modelling formalism we found that two very simple constructs, called TODO (do what there is to do) and DODOM (ritualized dominance interaction) are very versatile in generating "interesting" social structures. These constructs are described in section 3. The potential of these constructs is demonstrated in the sections that follow: in section 4 we summarize our previously published results on an individual oriented model of the social interaction structure of bumble bees, treating it as a special case of the principles set forth in section 3, in section 5 we show (by extending on the bumble bee paradigm) that social structures generated by TODO and DODOM are self-regulating and in section 6 we sketch how TODO and DODOM can be implemented in models of very different species: in contrast to bumble bees we take monkeys as an example. On the basis of this evidence we derive the theory that TODO and DODOM in combination can form the basis of the social organization in groups of animals.

We have deliberately defined socioinformatic processes in terms of interactions and effects, and not in terms of the type of entities in which they occur. This creates the possibility for the interpretation of other phenomena (e.g. cellular or molecular genetic) within this framework and makes it feasible for non-socioinformatic processes to shape the organization of "social groups" (e.g. ecoinformatic processes as defined above). In this paper we shall focus exclusively on socioinformatic processes in groups of animals.

2. Modelling formalism

> "As large as life,
> and twice as natural..."
>
> Lewis Carroll
> *Alice Through the Looking Glass*

As we mentioned above a modelling formalism for socioinformatic processes should allow for the separate definition and existence of spatio-

temporal entities (individuals). Individuals differ from "subsystems", "modules" or "blocks" used in classical modelling formalisms in that such units can function only when interconnections between them are established *a priori* (i.e. they are defined as parts of a whole (Hogeweg & Hesper, 1979)). However, such *a priori* fixation of the interconnections would preempt the purpose of socioinformatic modelling. Therefore the behaviour definition of an individual should include the establishment, maintenance, modification and termination of interactions with other individuals.

Another requirement of the modelling formalism is that individuals can be equal in a well-defined, non-trivial sense and yet differ in their behaviour. This can be achieved by defining the behaviour of an individual in relation to the environment. The concepts of MIRROR modelling (Hogeweg & Hesper, 1979, 1981*a,b,c*; Hogeweg, 1984) can be used to satisfy these requirements.

In a MIRROR model a universe is created consisting primarily of SPACEs (subdivided into PATCHes) and DWELLERs. DWELLERs are related to SPACEs in two ways: DWELLERs dwell in SPACEs and they support a SPACE: their 'skinSPACE' (e.g. mental space). The embedding of DWELLERs in SPACEs provides a mechanism to define the behaviour of a DWELLER in relation to its environment. The skinSPACE provides a mechanism for differentiating DWELLERs that are otherwise equal in an unlimited way and yet keeping up the notion of equal DWELLER.

Interactions between DWELLERs are established on the basis of nearness in some SPACE, i.e. DWELLERs can meet and who they meet depends on their behaviour pattern (e.g. their movements) in that SPACE, the presence and the behaviour pattern of other DWELLERs in that SPACE, and on the topological constraints of that SPACE.

DWELLERs can "shape" their environment, i.e. they can leave traces in the SPACE in which they dwell. These traces can be new DWELLERs (identical to or differing from the one who generates them); they can be PATHs, i.e. a special type of DWELLER which is formed and maintained by being trodden on, or SCENTs, also special types of DWELLERs which diffuse and dissolve. Alternatively, traces can be DEMONs. DEMONs are not DWELLERs and do not dwell in a SPACE and cannot be observed directly (as DWELLERs can be) by DWELLERs. Instead they live in a "shadow world" but are connected to "this" world via their TARGET and their TIE. The TARGET defines the circumstances which "revive" the DEMON, who then takes temporary control of the TIE, changing it and/or reviving it. Thus the DEMON can make a DWELLER do things "in spite of itself and without knowing" (i.e. the DWELLER does not contain code for this behaviour) or can cause a DWELLER to notice things which would

otherwise be overlooked (in that case the DWELLER does whatever its code dictates).

Not only do DWELLERs shape the space in which they dwell but they can also shape skinSPACES of themselves and of those they meet by means of the same mechanisms as those discussed above. Thus they can modify themselves and others. In this way a high order recursive redefinition of individuals is achieved.

Configurations of DWELLERs in a SPACE can be mapped into a (property of a) DWELLER (e.g. its location in SPACE); SENTINELs (a PATCH-bound type of DEMON) perform these mappings. Thus configurations of DWELLERs can become observable properties (e.g. the location) of DWELLERs in other SPACEs.

We think (Hogeweg & Hesper, 1979, 1981 a,b,c, 1983) that these mechanisms can go a long way in representing/generating behaviour and mental processes as versatile as those sometimes observed in humans, and yet they are of the same form as the minimum mechanisms needed to represent/generate the behaviour of (simple) animals.

There can be many species of DWELLERs in a MIRROR world, each being defined by a different behaviour pattern. Some are able to observe each other directly, some interact only through certain traces, whereas others do not interact at all. For socioinformatic processes, however, we limit the DWELLERs in spaceSPACE to one species, thus defining a simpler system which should show us the limitations of purely social (i.e. one species) systems as distinct from more diverse multispecies systems (such as those occurring as ecosystems or as cells). Note that it is always tempting to define a formalism in such a way that entities are generalized as far as conceivable, thus ending up with one type of entity or a very few types. If the entities are to be able to modify their behavioural definition (as in our case) then we could go very far in this reduction but this would mean that we would need more complex mechanisms for differentiation, or a more complex initiation of the universe. We have found that it is heuristically useful to distinguish different species possessing a relatively fixed behavioural pattern and study differentiation between them in a local way (i.e. relative to this prior definition). In this sense our modelling formalism seems to agree with evolution.

MIRROR, as described above, is a set of language independent modelling concepts, MIRSYS is a program written by us in Interlisp which defines a program environment in which MIRROR worlds can be shaped by defining the appropriate entities. In MIRSYS (which is itself a fairly large program) the definition of a particular MIRROR worlds can be fairly concise (e.g.

the bumble bee world (section 5) is not more than 6 pages "pretty printed" LISP code).

The entities forming the MIRROR world, e.g. SPACEs, DWELLERs, DEMONs, SENTINELs etc.) are (by MIRSYS) defined as Interlisp functions which contain explicitly an indirect reference to their own entry point (using the spaghetti stack facilities of Interlisp), called the ME pointer: ME points to a lisp atom whose name is the identification of the individual and whose value is the current entry point address. By this mechanism the functions can become entities (individuals), many of whom can coexist in the system and which can observe each other if they meet, i.e. if they obtain a reference to the other's identification (a YOU pointer). Such a YOU pointer can be obtained on the basis of its position in a SPACE, PATCHES being lists of entities contained in them.

In MIRSYS being the same kind of entity means being a reincarnation of the same Interlisp function, which includes a behavioural definition and local variables, but has a different identification, address, and values of local variables; the entity can, moreover, have obtained a modified behavioural definition through the configuration of entities in its skin-SPACE.

Entities are active "once in a while". The scheduling of their revival can be part of their behavioural definition but revivals can also be affected by anyone containing a YOU pointer to the entity; in particular they are often effectuated by DEMONs and in the case of DEMONs by the occurrence of certain situations defined in relation to their TARGET. DEMONs are attached to entities or variables or procedures through their TARGET and are always revived whatever happens to that TARGET (this revival is effected by the basic access and activation procedures of MIRSYS). The DEMON then decides whether the situation fits the circumstances required for its operation. If it does, the DEMON influences its TIE by changing it or reviving it.

Each MIRROR entity has a variable in which the cause of the revival is noted; its code determines how this information is used, i.e. the same types of entities use the same encoding/decoding procedure for this information, but different types can interpret this information differently.

MIRROR worlds differ from most other complex model systems in that they "live" on side effects (e.g. on the traces left in SPACEs and by DEMONs). We think that that is what life is about. If so, this should be incorporated in our theories on e.g. evolution, as will be shown in the subsequent sections.

3. Two Basic Principles for Socioinformatic Processes

3.1. TODO, DO WHAT THERE IS TO DO

As mentioned (section 2) the behaviour of the basically equal individuals should be defined in relation to their environment. The TODO principle is the simplest possible implementation of this requirement: the behaviour of an individual is triggered by what it encounters. Thus the individuals react in a simple "stimulus–response" manner, possibly modulated by a memory factor (e.g. DOM, the variable updated by DODOM, section 3.2.). Nevertheless in a sense its behaviour goes far beyond that of a simple automaton because: (a) it is not alone, (b) it and the other entities shape the environment, and therewith what there is to be encountered and (c) it has only local information, i.e. the available information differs for the various individuals and depends in an implicit way on previous behaviour (which determines where it' is).

A very simple example of the complexity generated even by meeting (the traces left by) "oneself" are "Patterson's worms" (Beeler, 1973; Gardner, 1973; Hogeweg, 1976): by letting the path taken by a worm be influenced by the pattern of eaten and uneaten paths which it encounters (and which it produced itself before), intricate walking patterns emerge which are entirely unpredictable or exhibit a regularity with a periodicity far longer than the memory of the worm (if it has any) (e.g. a 2 step memory generates a repetitive pattern of 1634 steps).

The TODO principle interfaces non-socioinformatic factors with the socioinformatic process because the former also shape the environment and thereby what there is to do. Such factors are for example: the availability of food, ontogenetic and population dynamic parameters of the animals involved, etc. We will show (section 5) that the TODO interface between such external factors and the social interactions generates a "self-regulating" social structure by which a viable group persists not withstanding external disturbances.

We want to stress that the TODO principle is much simpler (in fact it was originally used in MIRROR worlds for minimization reasons) than other mechanisms for alternative behaviour patterns of individuals of the same species (e.g. genetically mixed stable strategies) because most behaviour involves interaction with other entities and they have to be available and have to be found in order to be able to perform the behaviour (e.g. one cannot enter a barrow without there being a barrow) (compare Brockman, Grafen & Dawkins, 1979).

3.2. DODOM, RITUALIZED DOMINANCE BEHAVIOUR

The very definition of socioinformatic processes implies several con-
straints on the interactions between the individuals. For example, the
interaction should cause differentiation, but the differentiation should be
limited so that the individuals of the group can continue to interact. This
indicates that the interaction has the form of a damped positive feedback.
Such a damped positive feedback can be realized by an interaction the
strength of whose effect is inversely related to the strength of its cause. A
social interaction in which cause and effect are so related may be called a
ritualized interaction. We propose that a "ritualized dominance interaction"
(called by its modelname: DODOM) is a basic constituent of socioinfor-
matic processes in a wide variety of organisms ranging from bumble bees
to monkeys. In fact DODOM can be seen as the simplest example of a
socioinformatic interaction because in its interaction it uses only one variable
and random noise.

A DODOM interaction involves the following phases:

1. Assessment of the value of the dominance variable (DOM) of the
interaction partners.

2. Determination of the "outcome" of the interaction (who "wins").

3. Updating of the value of the DOM of each of the animals.

ad 1. In the most simple implementation of DODOM the DOM variable
is a property of the animals which can be directly sensed by all the
other animals (e.g. a pheromone); in more elaborate cases it is a
property of the animals which is generated in the interaction event
from the memory that the interaction partners have about their past
interactions.

ad 2. The outcome of the interaction depends on the displayed values of
DOM and possibly on other circumstances at the time of the interac-
tion; in the simplest case these circumstances are regarded as random
variation.

ad 3. The updating is such that the above-mentioned requirement of ritualiz-
ation is met: if the outcome of the interaction is in accordance with
the established (strong) dominance relations the existing dominance
relations are slightly reinforced, whereas in the, less likely, case that
the outcome is contrary to these relations (i.e. the less dominant animal
wins) this event causes a sharp change in the dominance relations. If
the dominance of the interaction partners is about equal, an intermedi-
ate amount of updating is enacted. In the simplest case the updating
is accomplished by a direct mapping in the DOM variable, in more

elaborate cases it is accomplished through a reconfiguration of the skinSPACE (compare: "memory", "self-image", "worldview" and the like).

It should be stressed that ritualized dominance is here defined in an informatic sense and not in terms of its physical implementation. The latter can of course vary greatly between different species while the informatic process remains identical. West-Eberhard (1983) argues that much morphological and behavioural variation among closely related species has evolved as a result of sexual and social selection. Her discussion seems to presuppose a rather invariant social structure: the selection affects the physical implementation rather than social structure. Thus the latter remains invariant in spite of the selection of the performance of the individuals, i.e. the social structure is apparently resistant to scale changes. We will show that ritualized dominance also shows such invariance.

We also should stress that socioinformatic processes can, of course, be coupled directly to other processes. For example a variable involved in the ritualized dominance interaction, which is being updated as described above, can also be changed by external factors, e.g. age, health, hunger etc. In addition such a variable can be restricted to a certain range by genetic or acquired factors.

As a paradigm system we shall, however, study socioinformatic processes in their simplest and purest form. Thus we assume that all individuals start in exactly the same state and that external factors have no direct influence on the variable involved in the socioinformatic process. We shall show that even under these circumstances the effect of ritualized dominance interactions depends on external factors, which therefore help to shape the social structure (i.e. the social structure is a "side effect" of the external factors). This is because the effect of ritualized dominance interactions depends crucially on who interacts with whom and on the previously established dominance configuration of the group, which can depend on external factors and/or on the population dynamic structure of the group.

4. Socioinformatic Processes in Bumble Bee Colonies

As an example of the versatility of the basic principles of socioinformatic processes described above (section 3) and of how these principles can be implemented in a model of the social structure of a particular animal, we summarize and expand in this section our previous results (Hogeweg & Hesper, 1983) on the social structure in bumble bee colonies which can be generated entirely by (an implementation of) these principles.

4.1. STRUCTURE OF BUMBLE BEE COLONIES

Bumble bee colonies are annual; in the spring the queen, emerging from hibernation, establishes a nest, performs all duties of nest maintenance and forages by herself. When the first brood emerges, the workers take over the tasks of foraging and nest maintenance and the queen concentrates on egg production. Thus, although bumble bees are capable of leading a solitary life (at least early in the season) a social structure forms.

Eggs are laid on young pupae so colony growth is essentially exponential but somewhat discontinuous since pupae become available in batches. The queen produces all offspring until late in the season and this offspring consists exclusively of workers. By the end of the season, however, the workers start to rear new queens (the difference between workers and queens is developmental and depends on the amount and composition of the food of the larvae), and start to lay eggs themselves. Worker eggs are unfertilized and develop into drones. At this time the queen also starts to lay unfertilized eggs, but usually she is soon thrown off the nest by the workers. Thus, a switch from worker production to generative offspring production occurs at the end of the season. It is well known that from an ergonomic viewpoint it is indeed optimal to produce working offspring as long as possible and then switch to generative offspring because that way a maximum worker force is available for generative offspring production (Oster & Wilson, 1978). These authors pointed out, however, that it should be hard to obtain an external cue for the timing of this switch because it takes 3 weeks to raise the generative offspring and during these weeks food should still be abundant.

The cue for switching from worker production to generative offspring production seems to be an internal one based on socioinformatic processes in the colony.

Van Honk & Hogeweg (1981) studied the social structure of a bumble bee nest throughout its development. To this end each day all interactions between adult bees were scored for half an hour with respect to the outcome of the interaction, defined as who gives right of way to whom. They defined social structure in terms of the dissimilarity of individuals with respect to their interactions with all other individuals of the nest (van Honk & Hogeweg, 1981; Hogeweg & Hesper, 1982). Using pattern detection techniques (in particular cluster analysis and principal component analysis) they found that:

1. There are two groups of workers: the elite group and the common workers.

2. Individuals start their life as common workers; some enter the elite group at a certain age. At the time of their entry in the elite they interact more than expected with the queen and other elite workers; once they are members of the elite they remain so till senility.

3. Only elite workers lay eggs at the end of the season and perform associated duties in the nest.

4. The queen is just as dominant over each of the workers at the time of her departure from the nest as before, but the size of the worker force is then such that each of the workers experiences less of this dominance.

5. After the departure of the queen the social structure of the nest deteriorates and chaos reigns.

Additionally it is known that the queen and some workers produce a pheromone which inhibits the ovary development of other workers (Röseler *et al.*, 1981).

4.2. SOCIOINFORMATIC PROCESSES IN BUMBLE BEES

In order to study how this rather intricate social structure can be generated by a simple socioinformatic process, we developed a model based on individual interactions between bumble bees (Hogeweg & Hesper, 1983). We set up a MIRROR universe consisting of a nest-SPACE which represents the comb and in which a species of DWELLER called BUMBLE lives. BUMBLEs can differ with respect to their developmental stage (their development is modelled as movement through developmental space divided into the PATCHes: *egg, larva, pupa, worker, drone, newqueen* and *queen*), and with respect to several parameters, most notably their DOM. The nest-SPACE consists of discrete PATCHes: the *centre, periph, pot* region and *outside*. The universe is initiated with these spaces and one BUMBLE in state *queen* (hereafter we will shorten "BUMBLE in *queen*" to QUEEN, etc.). The QUEEN starts her life as queen by building a cluster of eggcells and laying EGGs in them. The BUMBLEs then start moving through developmental space. While they are in *larva* they are fed; while they are in *pupa* they serve as substrate for eggcells. Once they reach *worker* they take up their duties in the nest.

The two main assumptions about the behaviour of the adult bees in this model are those set forth in section 3 as general principles for socioinformatic processes:

1. The TODO principle: The bees do what there is to do, i.e. their actions are triggered by things they encounter.

2. The interactions between adult bees are ritualized dominance interactions (DODOM). Several behaviour parameters depend on the variable involved in the DODOM interaction. In particular: activity of the bees,

position in the nest (i.e. time spent in *centre* en *periph*), amount eaten, inclination to go foraging all depend on that variable; the laying of eggs by workers depends on the change in that variable during the period of cell building.

For bumble bees on the comb, TODO takes a particularly simple form: encountering any entity on the comb (i.e. bumble bees in various stages of development) leads to one specific behaviour pattern and no activity is triggered by more complex configurations of entities (the latter would require pattern processing by the bees). Accordingly, TODO is implemented as follows: when a bee becomes active it chooses randomly one of the entities occupying the part of the nest which it occupies itself, and performs the associated actions. When finished (possibly in an other patch) the next random choice of an entity is made (etc.). (Note that this simple implementation allows a BUMBLE to meet itself, this is interpreted as being idle). Apart from this, an event in its skinSPACE, which represents hunger, can trigger a BUMBLE to go to *pot*: foraging depends on what it encounters there (honey or an empty pot).

The spatial differentiation made (*centre* and *periph*) is the minimal spatial differentiation which leads to the social differentiation of the nest: if TODO operates in a non-spatially differentiated nest, DODOM does not lead to the formation of a stable elite.

In bumble bees DODOM is defined as follows:

1. Observation

Each bee has a variable DOM which at eclosion is set to a value that is identical for all BUMBLEs (only the QUEEN starts off with a DOM of higher value). The value of the DOM variable of an interaction partner is observed through the antennating which precedes the decision of the outcome of the interaction (which agrees with the experimental findings of van Honk & Hogeweg (1981)). DOM might be observed as pheromone concentration.

2. Outcome of the interaction

The outcome of the interaction is determined on the basis of a random drawing from a uniform distribution between 0 and 1 and on the basis of the dominance ratio of the interacting bees:

$$if \ RAND(0, 1) < DOM_1/(DOM_1 + DOM_2) \ then \ k = 1 \ (bee \ 1 \ wins)$$
$$else \ k = 0 \ (bee \ 2 \ wins).$$

3. Updating

The new value of the DOM variable of each of the interacting animals

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FIG. 1. Protocols of the QUEEN, an elite worker and a common worker (classification derived from principal component analysis) from time = 70 to time = 72 in the nest represented in Fig. 2(a).

is calculated from their old values and the outcome of the interaction as follows:

$$DOM_1 := DOM_1 + (k - DOM_1/(DOM_1 + DOM_2))$$

$$DOM_2 := DOM_2 - (k - DOM_1/(DOM_1 + DOM_2))$$

We have shown (Hogeweg & Hesper, 1983) that in the MIRROR world the so defined ritualized dominance behaviour of the bees on the comb generated the social structure described above for live nests, i.e. we studied the MIRROR nests using the same methods as we used for experimental nests (see section 4.1) and obtained identical results.

The MIRROR world can also be observed in ways other than those used in the experimental work. Figure 1 shows protocols of the behaviour of three BUMBLEs of the MIRROR world: the QUEEN, an elite WORKER, and a common WORKER. The protocols show that the social position affects not only the interaction behaviour that defines the social position but also the other activities of the bees: The QUEEN spends her time "inspecting" but not handling EGGs and LARVAe, dominating (elite) workers and, (in certain periods) ovipositing; elite WORKERs are mainly concerned with feeding LARVAe (including getting honey at POT and building cells), whereas common WORKERs are less active but are more inclined to go foraging. Similar correlations between social position and the various activities have been observed by van Doorn (van Doorn & Hogeweg, 1983) who recognizes so-called "Neben activitäten" including building activities, cell inspection and eating of eggs. These are done exclusively by elite workers, whereas common workers do most of the foraging.

5. Buffering Capacity of Socioinformatic Structures

5.1. INTRODUCTION

Socioinformatic processes such as those described above are a means of "buffering" environmental or individual variation. Examples of such regulatory mechanisms in MIRROR worlds are described below, using the bumble-bees world described in section 4.

5.2. SWITCH FROM WORKER PRODUCTION TO GENERATIVE OFFSPRING PRODUCTION

Van Honk & Hogeweg (1981) concluded that the queen is just as dominant at the time of her removal from the nest as she was before but that the force of worker numbers causes her to lose control. This view has been

challenged on the grounds that the size of the nest can differ greatly and that generative offspring are sometimes seen in small nests (van Blom, 1985). In the MIRROR world this observation is compatible with the idea of force in numbers if the latter influence on the socioinformatic processes is taken into account, (see Fig. 2) because:

1. In slow-growing nests there are relatively few larvae and therefore, due to the TODO structure, encounters between the (elite) workers (and the queen) are frequent; a strong differentiation will develop in the DOM value of the workers; those with a very high DOM value will spend much time in the *centre* interacting frequently with the queen, creating a situation which for the queeen resembles the situation with very many workers (which leads ultimately to her removal) (Fig. 2(b) and (c)).

2. Contrariwise if the nest grows very fast the workers have little time to interact with each other or with the queen; the resulting dominance hierarchy is weak and less invariant in time; therefore the queen can tolerate a larger nest size before she is removed or killed (Fig. 2(a)).

3. The dominance hierarchy develops under the infiuence of the differences in the DOM values of the members of the nest. The ritualized dominance interaction is such that if for example the nest is started with a relatively dominant queen workers will develop a stronger dominance (they are "pulled up" by the queen) than when there is a less dominant queen. Moreover, if some workers start their life with a higher dominance value than others, their presence will be equilibrated by the socioinformatic processes. Thus, the ensuing social structure, and therefore the timing of the switch, will be relatively independent of such (genetic) variation.

FIG. 2. Buffering of the time of the switch against variation in the growth rate of the nest. Three simulated nests are shown. For parameters see Hogeweg & Hesper (1983) Table 1. The three nests differ in one parameter only: POVI, the probability that the QUEEN does not lay another EGG on a PUPA after the laying of an EGG. Of each nest the figure shows a) the nest composition over time (timesteps correspond to "days" via the population dynamic parameters) and the time of the switch (killing of the QUEEN), b) the value on the first principal component of the QUEEN (number 100) and the WORKERs ordered according to age and c) a dendrogram representing the similarity in interaction structure of the QUEEN and the WORKERs. Egg laying workers are marked *. The corresponding figures are represented on the same scale. (a) POVI = 0·6: The case described in Hogeweg & Hesper (1983); The QUEEN is much more dominant than the elite workers, but because of the large number of elite workers the QUEEN is killed at time = 73·875. (b) POVI = 0·9; Three workers develop a large dominance and resemble the QUEEN. Notwithstanding the small numbers they kill the QUEEN at time = 70·063. (c) POVI = 0·95: Stagnant growth: one worker (116) develops a large dominance (in the end almost as large as the QUEEN) and pushes the QUEEN off the comb at time = 54·073. Thus, over a large variation in growth rate of the nest, the timing of the switch remains fixed. Only for stagnant nest growth does the switch occur earlier (instead of later as the first order expectation would be), (compare van Blom (1985) who reports an early switch in slow growing captive colonies).

Thus, the time of the switch from worker production to generative off-spring production can remain fairly invariant under the influence of random, environmentally induced or genetically induced, variation. Such invariance is of course necessary if the population structure is to be used as cue for clocking the switch at the end of the season. Invariance is needed because of the relative independence of the cue and the "purpose" (i.e. to produce workers till the last but one brood of the season).

5.3. COMPENSATORY FEEDING

If the worker force is suddenly diminished (leaving the brood intact) "compensatory feeding" occurs in the MIRROR world as well as in captive bumble bee nests. Pendrel & Plowright (1981) described this phenomenon in a captive nest. They found that by halving the worker population, about half of the expected reduction in the feeding of the larvae was compensated by the more frequent feeding behaviour of the remaining workers. They attributed this to a simple reinforcement mechanism (after inspection of the amount of food that was left the larva was fed or not fed). However, compensatory feeding also occurs in the MIRROR world in which no such reinforcement mechanism was incorporated ("inspection of the amount of food" was not incorporated). In the MIRROR world it is caused by the TODO ("do what there is to do") principle: the decrease in worker force causes a decrease in worker/worker interaction to the advantage of the feeding of the larvae. Quantitatively this mechanism can result in a compensation similar to that observed by Pendrel & Plowright: half of the reduction is compensated if one-third of the worker force is removed from an average MIRROR nest at about time = 60. However, in the case of the MIRROR world the effect depends crucially on the composition of the nest; we do not know whether this is also true in live colonies.

In MIRROR worlds after some time the compensation will be compensated: the dominance hierarchy among the remaining workers is disturbed and many workers decline in dominance. The resulting loss in overall activity causes a slowing down of the rate of feeding: it may look as if the bees get tired. In such a situation we should expect loss of brood (e.g. by removal of larvae and/or starvation) resulting in a decrease in ovipositions, and finally in the recovery of a balanced nest structure.

Compensatory feeding leads (in the MIRROR world) automatically to compensatory foraging: the BUMBLEs go to *pot* more often (having exhausted their food supply) and find it more often empty. Compensatory foraging leads, in its turn, to a still farther reduction of the number of workers on the comb, who, therefore spend even more time feeding the

larvae. Nevertheless, compensatory foraging, leads, after a delay, to a reduction of the amount of feeding of the larvae.

Thus, the socioinformatic processes cause a short-term as well as a long-term regulation of the nest structure. They should have an effect in evolutionary time as well (Heringa & Hogeweg, 1985).

6. Socioinformatic Processes in Monkey Groups

6.1. INTRODUCTION

The data we have on monkey groups (live groups as well as simulated groups) are by no means as detailed as the data on the bumble bees of the previous section. In this section we simply sketch how the ideas outlined above could be applied to the analysis of the social organization of groups of higher animals such as monkeys.

Several "social strategies" such as "nepotism" "conservatism" have been distinguished (e.g. Moore, 1978; Jolly, 1972; Wilson, 1975) and discussed with respect to their adaptive value to certain environments. An analysis in terms of the socioinformatic process which generates the characteristics of these types of social organisation as an indirect response to different environmental conditions seems to be feasible, and may replace an analysis in terms of the advantages of such social organisations in different environmental circumstances.

A first step in this direction was taken by Hausfater, Saunders & Chapman (1981), Hausfater, Altman & Altman (1982). They analysed a Markov chain model in which rank changes in groups occurred with certain probabilities depending on population dynamic events (birth, death) or on aggression. The transition probabilities were varied. They concluded that the same model can generate various strategies if these probabilities are varied and that therefore no separate mechanisms are needed to generate such strategies. Assuming that these parameters change with changes in environmental conditions then this model is indeed a model that incorporates a causal rather than an adaptative line of reasoning. However, it is a very global model and therefore almost "begs the question": which informatic processes, i.e. which interactions between the individuals, lead to the change in the Markov chain probabilities?

6.2. DODOM IN MONKEY GROUPS

In this section we sketch a form of ritualized dominance interaction in which the observation and the updating step are more elaborate than in the case of the bumble bee interactions discussed above.

We suppose that in monkey groups individuals know each other, i.e. they possess a representation of each other in their skinSPACE. The simplest way to modify the DODOM interaction described above for bumble bees, so as to use the memory of past personal interactions instead of direct sensing of a dominance variable of the interaction partner is to assume that each animal has an estimate of the dominance variable of every other animal in its skinSPACE. In an interaction, the animals display on the basis of the dominance relations in their skinSPACEs instead of on the basis of the sensed ratio of the dominance variables. The outcome of the interaction depends on the displayed dominances, which, unlike directly sensed dominances, are not necessarily complementary (i.e. do not add up to 1). The updating now depends on the skinSPACE dominances, the outcome of the interaction and on the discrepancy of the displays, and it involves a change of position in the skinSPACE of both the animal itself and its interaction partner. The change of the position of the animal itself in its own skinSPACE modifies its future dominance interaction with all other animals, whereas the change of position of the interaction partner in the same skinSPACE only modifies the original animals future interactions with that partner. Note that in this modification of DODOM the memory structure is a substitute for the direct sensing of the dominance relations. This substitution may result in the formation of social substructures which (slightly) diverge from the global hierarchy; this depends on the environment which influences who meets whom. More importantly such a memory based dominance display can be modified by the circumstances, e.g. by which other animals are nearby (see below).

SkinSPACEs may in addition contain information about social connections between animals (e.g. kinship); if so, the displayed dominance is generated not only on the basis of the estimated dominance of the interaction partner, but also on the estimated dominance of "kin" nearby in space-SPACE. The outcome of the interaction then consists of who wins and who participated, the latter, influencing the former. The updating of the social connection estimate depends also on who participated, and may take many different forms. It will be intriguing to study the effect on social structure of the following possibilities:

1. Local updating: the change of one social connection estimate does not change estimates on other social connections.

2. Space dilating updating (compare Ward's clustering criterion, c.f. Hogeweg & Hesper, 1981d): an intensification of one social connection estimate leads to a relaxation of the estimates of the (estimated) less intensive social connections of the pair of animals under consideration, i.e. "if those are close friends the others cannot be close friends as well".

3. Space contracting updating (compare single linkage clustering criterion): the opposite of 2. i.e. "friends of its friends are its friends".

The effects of these different skinSPACE structures we have not yet studied but we suspect that the simplest ones can generate the rank changes described by Hausfater *et al.* (1982), e.g. 1) the rank decline of a mother can lead to the ascent in rank of the daughter although normally a daughter acquires a rank just below her mother and 2) subgroups which have joined a main group attain en bloc a social rank in the group.

Thus, although we have no data which require the more elaborate possibilities, we think that these should be investigated in order to find out whether such skinSPACE representations can have an observable effect on the social structure, and thus, instead of trying to find a minimal representation for observed social structures, we will work the other way around and try to find relevant observables for social structures based on skinSPACE representations.

7. Discussion

The central theme of our research is to show how simple interactions can lead to apparently complex structures. This theme we have studied before in the context of (morphological) development (Hogeweg & Hesper, 1974; Hogeweg, 1980) and of ecosystems (Hogeweg & Hesper, 1981). In all cases we have shown that the local interactions needed to generate complex patterns are far simpler than we might expect: human intuition about complexity fails utterly when faced with a transition from local interactions to the macro structures they generate.

In the models discussed above, behavioural patterns and social structure are generated by a combination of ritualized dominance behaviour and (via the TODO principle) the maintenance characteristics of the animals under consideration. Differences in social structure arise through differences in the environment in which the animals find themselves. The environment influences maintenance and developmental characteristics but does not influence the socioinformatic processes directly. Differences in social structure therefore do not have to be explained in terms of their adaptive value: they are only a side effect. Clearly, if the social structure so generated in a certain environment were to be disastrous the animal either would not occur in that environment or would evolve so as to evade the disaster. According to our analysis such an evolutionary process should primarily involve changes in the population dynamic parameters, since these are important in shaping the social structure of the group. However, these parameters are, of course, tightly constrained by other factors. Another possibility, according

to our analysis, is a change in "who meets whom" structure of the group although the possibilities are here restricted to what there is to do (and where). It is interesting to see that in social insects, individuals seem to avoid each other actively in certain circumstances, and if they meet nevertheless, they seem to ignore each other utterly (West–Eberhard 1969): the effects of the socioinformatic processes generated by interaction indeed seem to be detrimental in these circumstances (cf. West–Eberhard, op. cit).

Local interactions of autonomous entities generate macro structures in which intricate couplings exist between parameters and in which the set of alternative behaviour patterns is by no means continuous or obvious. This is not only true in social systems as studied here, but should be true also in the case of molecular interactions of which the macro structure is (ultimately) the organism.

Nevertheless a large amount of decoupling is assumed in most evolutionary theories: couplings between traits due to the interactions which generate the traits are mostly ignored, i.e. the theories consider one level of traits only (supplemented with a "pseudo" level of genes which is superfluous because of the assumed one to one mapping of this level to the studied traits).

In contrast we think that evolution is essentially a multilevel process. We conjecture that only by virtue of the informatic constraints generated by (the processes within) the organism itself, is an organism able to cope with its informatic needs. A simple example of this is the regulation of the switch from the ergonomic phase to the reproductive phase in the bumble bee colonies described above: only because of the causally spurious, but sufficiently strong correlation of the likely course of nest development with seasonality can the bees obtain a cue for this switch.

The mapping of this multilevel informatical interplay is the great challenge of bioinformatical research.

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(a)

(b)

(c)

Eggs

Larvae

Pupae

Workers

Drones
and
New Queen

Q killed

[facing page 324]