

Complexity and behaviour in
Leptothorax ants

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Social behaviour in ants of the genus *Leptothorax* is reviewed. Attention is paid to the existence of collective robust periodic oscillations in the activity of ants inside the nest. It is known that those oscillations are the outcome of the process of short-distance interactions among ants and that the activity of individual workers is not periodic. Isolated workers can activate spontaneously in a unpredictable fashion. A model of an artificial society of computer automata endowed with the basic behavioural traits of *Leptothorax* ants is presented and it is demonstrated that collective periodic oscillations in the activity domain can exist as a consequence of interactions among the automata. It is concluded that those oscillations are generic properties common to both natural and artificial social complex systems.

To my parents, with love and gratitude

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Preface

Complexity is the central problem of the so called sciences of complexity and is related to the properties that emerge from interactions amongst several elementary objects. It is related to the spontaneous generation of order that is present on different time and space scales from the one at which interactions occurs. This is an order generated without any central control or predefined plan either in the individual objects or in the local patterns of their interactions. This order emerges as a self-generated dynamic property and for this reason has been called self-organization. Self-organization often manifests itself by the spontaneous symmetry breaking of time and space patterns and by the possibility of highly organized collective behaviour in the absence of pre-ordained designs (Nicolis et.al., 1989).

Complexity, self-organization, emergent and synergetic properties are subjects undergoing an explosive growth of interest in many fields of science such as ecology, immunology, developmental patterns, neural networks, genetics, social behaviour, turbulence, lasers, computer theory, economics, chemical autocatalysis, etc. At the core of this explosion of interest is the realization that both natural and artificial systems (mostly computer models) are both quite capable of showing several complex phenomena in common. This, in particular has been of great interest in the study of life as a complex system through the new sciences of artificial life (Langton, 1989; 1991). What both natural and artificial life have in common are the processes that arise when simple objects (individuals or autonomous agents) are dynamically connected to each other in dense ways (Varela et.al. 1991). These objects (obviously discrete entities) can be cells, organisms or populations. Another feature of complexity is that emergent properties often manifest themselves in a hierarchical fashion: emergent properties are built-up over

the most basic space-time scale but other emergent properties can appear at other larger scales (Huberman et.al., 1985).

Self-organized systems could be studied using several mathematical formalisms, nevertheless over the past two decades it has been clear that traditional mathematical tools can not give full description of the richness of complex phenomena. This has forced the development of non-linear methods and specially those that are “naturally” suitable for the description of systems with many interconnected discrete elements: cellular automata, neural networks and coupled map lattices among others. What these models have in common is that they do

not treat the interacting elements in isolation since global collective properties can not be understood from the study of separate elements: self-organization is a holistic theory, the global features do not depend on the isolated microscopic mechanisms only and so global properties cannot be understood by analysing the parts separately (Bak & Chen, 1991).

Cellular automata, in particular, are perhaps the most simple of those models but they are well capable of several complex dynamical behaviours like self-organization and collective behaviour (Wolfram, 1986). A very good description for the suitability of CA as models for self-organization has been given by Varela and Coutinho (1991): “it is instructive to give a simple example of emergent properties: consider a cellular automaton, a simple unit which receives inputs from the neighbouring automata, and communicates its internal state to the same immediate neighbors. Assume that the cell or unit can exist only in the two states (1 or 0, active or inactive), and that the local rule governing the change in the state of each automaton is simply a logical function of inputs from each neighbor. Now connect a string of such elementary automata into a circular array, so that there is no fixed input and output to and from the entire ring, but only internal activities, which is typical of a network. Remarkably, even this minimal network shows rich self-organizing capabilities...The basic point here is that the emergence of global patterns or configurations in systems of interacting elements is not unusual. In fact, it seems difficult for any densely connected aggregate of cellular elements to escape from having emergent properties. This provides a long-sought for connection between different levels of description in biological phenomena”.

Social behaviour in insects seems to be a biological phenomenon quite suitable for being properly considered as a self-organized process. Insect societies are based on the existence of several social units (the insects) that interact among themselves producing global emergent co-operative behaviour. In fact the understanding of social behaviour as a collective property of a set of individuals is one of the major challenges in the current study of social insects (Camazine et.al., 1991; Cole, 1991a).

Clearly social behaviour cannot be reduced to the individual behaviour in the sense that isolated social units are unable to show collective behaviour. Social behaviour is thus holistic and synergetic and is only produced by the existence of more than one interacting organism. It is clear, on the other hand, that not all aggregations of individuals are social; social behaviour only exists if the interacting individuals can communicate with each other and can modify their individual behaviour as a consequence of such communication acts (interactions). Social behaviour has to do with some form of co-operation in the sense that two or more social units may do something together, that is, if two or more individuals can keep together reacting to each other acts and can engage in carrying out some common tasks.

Ants are social organisms that fulfil very well the above characterization of social behaviour. No matter that an ant has only very limited behavioural capabilities, the colony as a whole is usually a highly integrated structure and this colony-level order comes as the output of coordinated massive individual

interactions that are facilitated by the existence of effective communication links among them.

The present study concerns collective behaviour in ants of the genus *Leptothorax* but also concerns artificial societies. It deals with the new trend of considering natural and artificial interconnected systems as having a number of common generic properties, not because of the design details of their individual elements but because of the characteristic of being densely connected and because of the fact that the state of the individuals can be modified by interactions. In some degree, social behaviour must be regarded as the inevitable outcome of such interconnected structures and must be regarded as a robust generic property of natural and artificial self-organized complex systems.

In chapter two of this work, I will present some of the basic behavioural traits in *Leptothorax* ants. Most important will be the discussion about the existence of collective short-period oscillations in the activity patterns of such ants, that are thought to come from the interactions among individual workers. I will mention the remarkable finding that isolated ants can activate spontaneously following a pattern that seems to be chaotic and the oscillations are robust from the point of view of the number of individuals. In chapter three, I will develop a model of an artificial society whose elements will be computer automata. The mobile automata will be shown to exhibit collective oscillations that originate in the process of interactions. The presence of social facilitation will be studied as well as the space distribution of activity. The resemblance of collective behaviour in both automata models and ant colonies will be discussed.

I am grateful to the many people who made very useful comments about this work. Special thanks to Ricard Solé, Brian Goodwin and Graham Read. I appreciate the collaboration of the Open University ACS that offered very useful advice for the use of computer facilities. Special thanks to Craig Howard for information on using the transputer facilities. I am in debt with the British Council and the Universidad Nacional Autónoma de México, for the scholarships awarded. Many thanks to Caroline Pond for suggestions about the process of writing this work.

I can not stop to dedicate this work to all my dearest friends and to all the very helpful and kind people that help to make my living in Milton Keynes more easy. Special thanks to Tere and Tessy, Jonathan and Risa, Brian, Ricard, Christian and all the Wimpey II people. Also I appreciate the help from my friends who help me pass my feeling of isolation by sending warm messages through e-mail, thanks to Ricard, Omar, Raul, Faustino, Claudio, Angelica and Pedro. ¡Va por ustedes!

It must be said that the work presented here, with only minor changes, was submitted for the degree of M.Phil. at the Open University in Milton Keynes, UK, in September 1993. After this date, many new results on insect complex behaviour have enriched the field. The reader is then warned that this book discusses results up to that year.

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Chapter 1

Behaviour in *Leptothorax* ants

It may be said without ambiguity that the genus *Leptothorax* is, indeed, chaotic. Following the first common meaning of the word, myrmecologists acknowledge that the systematics of the genus is, at the present time, in a great state of confusion (Douwes et.al., 1991; Loiselle et.al., 1990; Heinze, 1989; Buschinger, 1981). On the other hand, and following the second meaning of the word, the ants of the genus may be chaotic in *sensu stricto*: at least this is the case of the spontaneous activation patterns of *L. allardycei* isolated workers that have been shown to exhibit low dimensional chaos (Cole, 1991b).

1.1 A brief taxonomical review

Almost 200 years have passed since P. A. Latreille, described as “by far the most important of the pioneers in myrmecography” introduced the term *Leptothorax* (Wheeler, 1960, p. 125). However the taxonomic status of this genus is still far from clear.

Taxonomists studying the genus have encountered many non-trivial difficulties in its description. For instance, environmental factors can modify different phenotypic characters traditionally used for identification and classification. This is the case of body coloration that depends on the temperature at pupation, a phenomenon found in many *Leptothorax* species (Plateaux, 1981, p.64). Another difficulty, among many others, is the fact that morphologically almost identical ant colonies, considered to be members of the same species, may have different chromosomal numbers as found in *L. muscorum* (Loiselle et. al., 1990). *L. muscorum* was thought for many years to be a single species. Today it is accepted that, rather than a single species, it is a compact group known as the “muscorum complex”. It is not surprising then that very active research work is being pursued to establish with precision the taxonomical picture of the genus. This effort has involved many different approaches including chromoso-

mal counting, electrophoretic analyses and species redescription (e.g. Heinze, 1991; Heinze, 1989; Snelling, 1986; Spadaler et.al., 1983, Buschinger, 1981;Plauteux, 1981).

Being aware of this, I will not attempt the road of giving extensive taxonomic details when discussing the biology of this genus. For the purpose of the present work it will be sufficient to say that the nearly 350 named taxa of the *Leptothorax* belong to the subfamily Myrmicinae and family Formicidae (Heinze, 1991) and that, within the Myrmicinae, a compact group of four genera is known as the Leptothoracine tribe: *Leptothorax*, *Doronomyrmex*, *Harpagoxenus*(=*Protomognathus*) and *Formicoxenus*. The ants from the Leptothoracine tribe are very closely related and share a number of morphological, ethological, and ecological characteristics. The tribe has been intensively studied in the past because of the existence, among their member genera, of social parasitism as I will describe in more detail below. Further, *Leptothorax* is divided into several subgenera. The best known and studied of these are the temperate North American and Euroasian subgenera: *sensu stricto* (*L. muscorum* complex, *L. gredleri*, *L. acervorum*); *Myrafant* (*L. ambiguus*, *L. curvispinosus*, *L. longispinosus*) and *Temnothorax* (Heinze, 1991). Recently, a previously Myrmicinae genus, the neotropical *Macromischa* has been included as a subgenera of *Leptothorax*. It includes, among others, *L. allardycei*, *L. laetaus*, *L. villarensis* and *L. isabellae* (e.g. Snelling, 1986).

1.2 Distribution

Leptothorax ants are distributed worldwide and occur almost everywhere (Wilson, 1974). These ants are commonly found in woodlands and forests. *L. acervorum* has been reported to exist in such high latitudes as Alaska (Heinze, 1991) and is represented in tropical latitudes by, among others, *L. allardycei* in the Florida keys and *L. isabellae* (Wheeler) in Puerto Rico (Snelling, 1986).

Leptothorax ants are usually described as small or tiny in size. With the exception of, perhaps, *L. acervorum* the ants of this genus are, in fact, among the smallest ants measuring around two to three millimeters or even less. Populations are very patchily distributed and can be extremely dense (Alloway, 1980; Aron et.al., 1986; Möglich, 1978). It has been found that colony densities of 2 to 3/m² are frequent in old nut falls under oak and hickory trees (Alloway, 1980).

Leptothorax usually nest under bark and in fallen wood, in moss, under stones, cracks in rocks, rock cavities, between wall stones and in fallen seeds like acorns and nuts (some species prefer to nest on trees). In general *Leptothorax* ants show a tendency to nest in preformed cavities since its nest construction capabilities probably score rather poorly as suggested by Herbers (1986a) for *L. longispinosus*. However it may be said that this capability is by no means absent since workers under laboratory conditions can be observed engaging in nest construction works, as noted by Provost (1989) in *L. lichtensteini* and Franks (personal communication) in *L. unifasciatus*.

Myrmecologists usually keep entire colonies living in between a pair of glass microscope slides. This, together with the fact that they can live in such small sites as hollow acorns, prompt us to discuss the size of a colony.

1.3 Colony size

Ant colony size depends strongly on the species under consideration and no single factor (environmental or intrinsic to the colony) has been found to explain the huge variety of sizes found across the known species of ants (Hölldobler et.al. 1990, p.160).

One of the most striking examples of large colony size is the Japanese *Formica yessensis* whose colonies can reach 307 million adults. The African *Dorylis wilverthi* can have around 22 million and the tropical American *Atta colombica* two and a half million. *Leptothorax* ants, in contrast, are undoubtedly at the other extreme in the rank of ant colony sizes. In fact, for ants used to living in hollow acorns colony size must be very small. If we were to consider a typical colony size of this genus, a value of around 100 would be normal (an example of colony sizes for different species is shown in table 2.1). However, it is necessary to remark that colony size depends, generally, on the age of the colony. Colony sizes of around ten are a good indication of a young colony. Mature colonies can have extreme maximum sizes of about 400 adults in the case of *L. acervorum* (Franks et. al., 1990) and around 500 in *L. unifasciatus* (Martin, 1991). Aron et.al. (1986) and Aron (1986) reported exceptional sizes of 780, 900 and 970 in *L. unifasciatus* under stable laboratory environment, but it is improbable that such a large colony size can be attained under natural conditions.

Presumably, maximum colony size is constrained to a level where it still can function and act as a self-regulated unit. Hölldobler et.al. (1990) have suggested that a correlation might exist between colony size and elaborateness and variety of the colony communications system. Also it has been suggested, and observed, that once a colony gets close to its maximum observed size, it engages in production of sexuals and undergoes a colony fission. Plateux (1981) reported that once a colony of *L. nylanderi* reached a size above one hundred the production of males was observed.

1.4 Social organization: queen number and role

The genus was described by Donisthorpe (1915, p.144) as comprising “very agile, robust, and hard ants, which however are of a timid and adaptable temperament, and not at all warlike in nature”. Apart from this description, inadequate in some cases and adequate in others, *Leptothorax* ants are usually described as being rather uniform from ecological and behavioural points of view. Nevertheless it is true that different species can have specific behaviour and social organizations.

Species	Workers ¹	Range	Colonies	Reference
<i>L. acervorum</i> (Fab)	80	12-216	4	Tofts et.al., 1992
”	42.8	21-69	7	Franks et.al, 1990
”	—	34-43	4	Franks et.al, 1987
<i>L. allardycei</i> (Mann)	—	20-120	—	Cole, 1991a
<i>L. ambiguus</i> (Emery)	40.3 ± 9.4 ^a	—	—	Alloway et.al., 1991
”	62.1 ± 8.4 ^a	—	—	idem.
”	14.4 ± 0.6 ^a	—	8	Stuart, 1991
”	28.4 ± 3.4 ^a	—	8	idem.
<i>L. curvispinosus</i> (Roger)	41.1 ± 29.6 ^b	10-165	258	Stuart, 1992
”	40.1 ± 23.7 ^b	10-95	20	Stuart, 1987a
”	50.9 ± 28.5 ^b	17-100	20	idem.
”	92.8 ± 91.2 ^b	8-375	20	Stuart, 1987b
<i>L. gredleri</i>	29.4 ± 21.6	up to 95	41	Heinze et.al., 1992
<i>L. italicus</i> (Consani)	8	8	1	Poldi, 1991
<i>L. lichtensteini</i>	—	20-50	6	Provost, 1991
<i>L. longispinosus</i> (Mayr)	45.4 ± 9.0 ^a	—	—	Alloway et.al., 1991
”	48.9 ± 8.7 ^a	—	—	idem.
”	36.3 ± 23.6 ^b	10-165	281	Stuart, 1992
<i>L. muscorum</i> (Nylander)	42.3	9-85	16	Stuart et. al., 1983
<i>L. unifasciatus</i>	119.2	60-184	5	Franks et. al., 1992

Table 1.1: Colony sizes for selected *Leptothorax* species. 1=average number, a=standard error, b=standard deviation.

If we are to follow Donisthorpe's "psychological" profile for *Leptothorax* ants, we should agree when we compare the behavioural habits of those ants with the rather impressive and hardly inconspicuous predatory activities of the tropical raider ants, such as *Eciton burchelli*, or with those noticeable and devastating habits of the slave-makers such as *Polyergus rufescens*. However we are forced to disagree when noting that *Leptothorax* ants can be territorial, have a well developed sting, and may engage in fighting (often enduring hours) when facing threats to the nest (Alloway, 1980; Stuart et.al, 1982a; 1982b; 1983); and that, in fact, slavery occurs at least in one of its species: *L. duloticus* (Heinze, 1991; Wilson, 1974; Alloway, 1980). Nevertheless it is true that for an ant of such size and with such limited colony sizes, "warlike" activities are not in its common behavioural repertoire. In fact, the size of individuals and the size of the colony influence strongly the behaviour and ecology of these ants: when facing attack *Leptothorax* ants usually do not fight to the end, but as the resistance decreases, colony members carry away part of the brood and avoid further battle by fleeing away and abandoning the nest (Stuart et.al., 1983).

Ants are mostly females. Males exist for brief periods only to mate and fertilize eggs. Females are of two different sorts, the workers engaged in the daily colony activities (nest maintenance, brood care, foraging, defense, etc.) and an individual (or several) specialized in reproduction and called the queen, a name that however appears to be inadequate, since she does not rule colony life (Chauvin, 1970; Gordon, 1992). Ant colonies (and this is true for *Leptothorax*) can have no queen, one queen (monogynous) or several queens (polygynous). Queenless colonies of *Leptothorax* are common in nature and it appears that they can occur in sizable proportions. Alloway et.al. (1982) reported that, of 1522 *L. ambiguus* colonies collected in the field, 29.7% were found to be queenless. Of 488 colonies of *L. curvispinosus*, 36.6% were queenless and of 640 colonies of *L. longispinosus*, 37% were queenless. The lack of a queen or the existence of several suggests immediately that queen(s) is(are) not essential for normal daily colony function.

Several aspects of social organization in *Leptothorax* are crucial for testing the validity of current theories about the origins of social behaviour such as kinship theory (Hamilton, 1964; Trivers et.al., 1976), one of the "keystones of sociobiology" as stated by Provost (1991). Thus is not surprising that most of the published literature in the last ten years on the ethology of this genus is devoted to the study of such behavioral phenomena as dulosis (or slavery) and social parasitism, nestmate recognition and polygyny.

Social parasitism in ants has evolved to the point that some species are not capable of feeding themselves or tending their own larvae and then rely on the workforce from other species (Heinze, 1991). Social parasitism starts when a recently fertilized parasite queen successfully penetrates the nest of another species without being rejected at all. Parasite queens often do not tolerate the host queen and kill or expel her as is the case of *D. goesswaldi*, a workless Leptothoracine species that parasitizes *L. acervorum* and perhaps of *L. wilsoni* and *L. paraxenus* that parasitizes *L. sp.B.* (Heinze et.al., 1991) In some other species, the parasite queen lives alongside the host queen as in the case of

L. faberi and *L. minutissimus*, that parasitizes *L. sp.D.* and *L. curvispinosus* respectively or *D. kutteri* (= *L. kutteri*) and *D. pacis* that parasitize *L. acervorum* (Heinze, 1991). The parasite queen lays eggs that are tended by host workers. Those alien eggs normally produce sexual offspring but not workers. When eclosed, alien sexual forms leave the nest to mate and the daughter queens complete the cycle by further invading other nests.

Dulosis or slavery occurs when slave-makers raid the nest of another colony (either intra or interspecific) and steal the pupae. Once the stolen pupae eclose, the enslaved workers are integrated to the work force of the slave-makers and carry out the normal colony work except that the brood tended, feeded and defended by them are not their own relatives. On some occasions enslaved ants participate in slavery raids against ants of their own species (Stuart et.al., 1983). Among *Leptothorax*, *L. duloticus* is the only known slave-maker and it enslaves ants of *L. ambiguus*, *L. curvispinosus* and *L. longispinosus* colonies (Heinze, 1991; Stuart et.al, 1983; Alloway, 1980; Wilson, 1974). Other Leptothoracine are well known slave-makers: species from the genus *Harpagoxenus* enslave *L. ambiguus*, *L. curvispinosus*, *L. longispinosus*, *L. acervorum*, *L. muscorum* and *L. gredleri* (Heinze, 1991; Stuart et.al, 1983; Alloway, 1980; Wilson, 1974).

Social parasites are often morphologically very similar to their hosts. This fact is reflected in what is known as “Emery’s rule” after the myrmecologist Carlo Emery. Today a version of this rule, slightly modified is widely accepted: parasitic ants and their hosts are phylogenetically closely related. This has been tested by means of electrophoretic methods. Preliminary conclusion points towards considering that social parasites and dulotic species of *Leptothorax* are, in fact, closely related and presumably diverged early in the evolution of the present genus (Heinze, 1991).

The existence of dulosis and social parasitism seems to contradict assumptions of kinship theory where kin recognition is essential for maintaining close genetic relationship. It is assumed that workers of an ant colony display “altruistic” behaviour caring for the queen brood because of a close relationship with their future sisters. Yet it seems difficult to explain why workers in a parasitized colony tend brood of a queen coming from a different species even when no close genetic relationship is present. Moreover, it seems difficult to understand why enslaved workers even participate in slavery raids against their original sister’s colony in order to increase the enslaver work force without the benefit of perpetuating their own genes and, on the other hand, decreasing their own inclusive fitness by promoting disruption by destruction of their sister’s colonies.

It seems then that the mechanisms of kin recognition are very weak and not foolproof at all. Not surprisingly the research on the mechanisms of nestmate recognition in *Leptothorax* has been very intense in recent years (Stuart, 1992; 1991; 1988; 1987a; 1987b; Jaisson, 1987; Hare, 1987; Plateux, 1985; Schumman, et.al., 1991; Alloway et.al., 1989; 1991a; 1991b; Provost, 1991; 1989).

It is accepted that nestmate recognition is generally based on chemical cues (odors) that are located on the ant’s body surface. These cues may have both genetical and environmental components and the colony signature is undoubtedly learned by colony members (e.g. Stuart, 1992; 1991). Adults are integrated

and fully accepted as members of the colonies after a short period of “acceptance” in which, presumably, either the chemical signatures of the new workers are learned by their nestmates or the newly eclosed members acquire cues for acceptability (e.g. Stuart, 1987a; 1987b). The existence of this “period of proof” is demonstrated by the well know fact that young workers can be easily transferred among intra or interspecific colonies and be accepted as nestmates. This was demonstrated by experiments like the one carried out by Stuart (1992) where mixed colonies of *L. curvispinosus* and *L. longispinosus* were produced by transferring newly eclosed workers between colonies. Dulosis is the best proof that this phenomenon actually happens in natural conditions.

The exact mechanism of nestmate recognition has been a puzzle for a long time and different explanations have been given to explain it. It has been proposed that cues are based on individuals, on the colony or imposed and controlled by the queen(s). But by means of adoption experiments in different species, it has been possible to refute the idea that nestmate recognition is based on individuals or controlled by the queen. The more plausible explanation then is that the mechanism is collective and distributed over the colony (Stuart, 1988, 1987a). Moreover, those findings seem to support the view that social-insect colonies could be more properly considered as “fellowships” of cooperating individuals based on familiarity as was originally proposed by Jaisson (1987) (see also Stuart, 1988).

Leptothorax ants are territorial and they usually defend vigorously the territories around their nests by attacking or repelling intruders. It is known that in *L. ambiguus*, the levels of “aggression” against non colony members is independent of the number of queens present in the nest and that the level of “aggression” is more intense in large than in small colonies (Stuart, 1991). The independence between queen number and “aggression” suggests that defense behaviour is not centrally controlled. On the other hand the fact that more “aggression” is present in colonies with more workers points toward considering it as a collective behaviour.

Another challenge for kinship theory is the existence in ant societies in general, and in *Leptothorax* in particular, of polygyny (Herbers, 1986a). Again, it is not a surprise that the phenomenon of multiple reproductive queens in a single colony is a very intense research subject and has been considered one of the most debated issues in insect sociobiology today (Heinze, et.al., 1992; 1990; Bourke, 1991; 1988; Herbers, 1986a; 1986c; Herbers et.al., 1983; 1982; Alloway, 1982; Plateux, 1981)). Polygyny seems to conflict with the view that workers participate “altruistically” in colony life because of the genetic relatedness to the brood. Nevertheless, the existence of multiple reproductive queens can decrease the degree of relatedness among colony members. Also, the existence of several reproductive females should induce “reproductive competition” and have negative consequences for the general efficiency of the colony (Heinze et.al., 1992; Frumhoff, et.al., 1992; Pamilo, 1990; Herbers, 1992, 1990; 1984;) a situation that challenges the theory of natural selection since it fails to explain why the monogyne state is not always favored (Heinze et.al., 1992).

Leptothorax ants are monomorphic, that is they have a single body morphol-

ogy, in contrast with other ants that have clearly distinct morphologies classes of workers, commonly called “castes”. In “caste”-organized ants, workers belonging to different morphological classes are usually specialized for specific tasks, although it is known that the roles can have some flexibility and task switching can occur under specific circumstances. In monomorphic ants, it appears that some degree of specialization develops in correlation with age where young workers are engaged mostly in tasks inside the nest while the older ones spend more time in external activities such as foraging, nest maintenance and defense. This situation is however very dynamic and ants have a range of behavioural plasticity to adapt to different situations, as is best exemplified in the process of nest foundation where the first workers to eclose, from the first generation of eggs layed by the founder queen, are forced to forage simply because they are the only ones. In *L. italicus*, the first eclosed worker was observed to spend the first day inside the nest mostly inactive and was ready to forage by the second day (Poldi, 1991).

In some *Leptothorax* ants such as *L. acervorum* it appears that rather than a queen to worker control, the opposite holds since it is frequent to observe workers of this species gripping queens to a degree that often inhibit their feeding. Bourke (1991) suggested that this behaviour could be an exercise of powerful worker-to-queen control aimed at regulating queen number. Also in this species it is common that workers feed upon queen-layed eggs without any opposition or defense on the part of the queen (Bourke, 1991). Moreover, queens in *L. acervorum* are commonly ignored by workers who pay little attention to their presence. This observation is important because it implies the lack of a “court” of daughters caring for the genetically related mother.

With the exception, perhaps, of *L. allardycei* normal colony life is not disrupted at all by the lack of a queen. In many *Leptothorax* species, workers are able to reproduce with or without the presence of the queen and in queenless colonies workers are more prone to reproduce. In queenright colonies worker-layed eggs are often eaten by the layer, other workers or the queen. It appears that *L. allardycei* is a special case of this, since queenless workers seems to organise in “dominance hierarchies” where older workers lay eggs and exercise “dominant” behaviour toward their nestmates. This might include “aggressive” displays (Cole, 1981; 1986; 1984; 1988).

1.5 Communications

Efficient communication channels are essential for the existence of ants as groups of organized social beings. Communication serves to acquire, share and distribute information about the current state of the colony and the environment and so is invaluable in coordinating and organizing the work of the several colony members. Ant societies have developed many forms of communication, not all of them carrying the same quantity or quality of information and thus they are used selectively for different purposes in different contexts.

Communications are usually classified by the nature of the signal carrier

as chemical, acoustical, mechanical or visual (Matthews et.al, 1978). They are also classified by the function they serve (alarm, attraction, recruitment, grooming, trophallaxis, recognition, etc. Hölldobler et.al., 1990). Here I will simply distinguish *Leptothorax* communication by its range: short-range and long-range.

By short range I will consider only those communications that occur over a distance so close that they only occur by direct body to body contact. This implies that short range communications are restrained to antennation, grooming and trophallaxis (including interchange of solid food). Long-range communications are those that do not require direct mechanical contact among individuals. These include pheromones, stridulation (both air and solid vibratory propagation) and visual signals.

Leptothorax are very compact and dense groups of ants that live in close proximity to each other, suggesting, that their communication systems are mainly restricted to short-distance. The ethograms reported elsewhere demonstrate that they commit a significant part of their time to communicating by direct mechanical ways (e.g. Herbers, 1983). This reflects also the nature of their social organization where there is no central hierarchical control and workers are in charge of distributing, perhaps in a self-organized way, tasks inside and outside the nest. This is further facilitated by the existence of close interactions.

The existence of close contact among colony members does not imply that *Leptothorax* ants do not have other means of communication available. Like all other ants, they have well developed glands capable of producing chemicals for communication purposes. Two of these glands are the poison gland and Dufour's gland, both located in the ant's gaster. The poison gland is a complex of filamentous glands that converge into a "poison sac" that acts as a poison reservoir (Hölldobler et.al., 1990). The function of this gland is the production of neurotoxic and/or histolytic substances employed in defense or predation and are applied through the sting by direct biting or by squirting, if the intended use is to cause alarm or attraction. Dufour's gland is a highly versatile organ involved in the production of a large variety of chemicals. It is not clear what specific functions these have, but they might mediate alarm, recruitment and sexual attraction (Hölldobler et.al., 1990).

In *Leptothorax*, the poison gland was found to be associated with a class of simple recruitment technique known as "tandem calling" (Möglich et.al., 1974; Hölldobler, 1978). When an explorer ant discovers a new food source, it runs to the nest where it shares the food with other workers by regurgitation, then it turns around and raises the gaster upward while exposing the sting with a droplet of an extruded liquid on the tip. Other workers are attracted to the calling ant. The first to arrive touches the caller on his legs or gaster with the antennae. When touched, the caller guides the recruited to the food area (In this recruitment technique, only one nestmate is recruited to the intended area). During the travel, the follower keeps antennating the leader. If for some reason the antennation ceases the leader stops and waits for the nestmate to reassume contact.

It is interesting to note that while "tandem calling" involves the use of

attracting chemicals, the process of close contact between the pair of ants is still present, reflecting again the fact that *Leptothorax* ants rely heavily on direct body contacts and interactions for communication purposes.

Further, the presence of a so called “trail technique” is known to exist in *Leptothorax*, at least in *L. unifasciatus*. It consists in the foraging ant laying a trail of chemicals (from the poison gland) from food source to the nest that other nestmates can identify and follow (Aron, 1986; Aron et.al. 1986). Moreover, it has been suggested that the ants can chemically modify the nest area so to distinguish familiar well explored areas from those new unexplored. Impregnation of ant colony odour can then explain also the fact that *Leptothorax* appears to be territorial.

Leptothorax ants also relay in trail for nest migrations. In *L. affinis*, a species that lives in trees, the existence of trails was found by Maschwitz et.al. (1986) but more remarkable was that the ants, while engaged in social carrying (adults carrying brood or even other adults), follow colony-specific trails, but also individual-specific trails. Workers did not follow trails left by other colonies of the same species but preferred trails of their own colony and moreover they preferred their own individual trails rather than those of their nestmates. Maschwitz et.al. (1986) concluded that “the colonies of this ant organize their foraging and other outside activities mainly individually. Therefore it is important for the workers to be able to find their own trails quickly and securely and to be able to distinguish them from the trails of other colony members. Recruited individuals come to know their routes directly by tandem running or social carrying without the need to use trails of nestmates.”

Other substances produced in the *Leptothorax* Dufour’s gland do not have the porpoise of serving as facilitators for orchestrated social behaviour; quite the opposite. It is known that the parasitic workerless queen *L. kutteri* (= *D. kutteri*) produces a substance that disrupts nestmate recognition in *L. acervorum* causing workers to fight each other while the queen infiltrates the nest avoiding attack by distracting attention from her. These chemicals have been call “propaganda substances” (Allies et.al., 1986).

Few studies have been done to identify with precision the chemical repertoires found in *Leptothorax* glands. It is expected, however that some of the substances would be similar due the close phylogenetic relationship, but other substances are expected to be different and species-specific. Ali et.al.(1987) have studied the contents of Dufour’s gland for *L. acervorum* and *L. nylanderi* and have found this trend. Various of the identified compounds were similar but others differed markedly. In *L. acervorum* there was a predominance of C_{17} compounds while in *L. nylanderi* the C_{15} predominated. It is interesting to note the fact that chemical analysis of queen and worker gland contents revealed no difference. This seems to give further evidence to the global idea that queens in *Leptothorax* species do not rule centrally the life of the colony.

It is quite possible that pheromones mediate sexual attraction in *Leptothorax* ants. It is known that *L. acervorum* shows nuptial flight and calling behaviour that consists in the female displaying a posture characterized by a straight but angled body with the gaster pointing upward and the sting extended (Franks

et.al., 1991). This is a typical posture that in related species is known to occur in association with the release of pheromones. Calling behaviour is also exhibited by *L. muscorum* and *L. gredleri*.

Another type of long-range communication mechanism is stridulation. In ants it is produced by specialized abdominal apparatus made of a series of fine undulated striations. A scraper located on a next abdominal position is rubbed against this surface (friction is produced by movements of the gaster). Stridulation produces vibratory signals that can be transmitted through the air as sound waves or, through the ant's body and legs, to the substrate. It has been long speculated that these signals can serve for communication purposes. Stridulation is produced in many circumstances but it is mainly known to be produced when an ant is trapped or forced to be motionless (e.g. Dumpert, 1978 and references therein). Stridulation is known in *Leptothorax* ants and has been intensively studied in *L. muscorum* (Stuart et.al., 1980). In this species, stridulation has been identified when the ant is involved in fighting, dissecting insects, in trophallaxis with adults and larvae or when moving larvae stuck to the substrate. It has been also identified to occur in food-deprived and water-deprived ants that consume liquid food or solid matter and when they groom other workers or larvae. Stuart et.al. (1980) suggested that, due to the variety of different contexts in which this behaviour is present, their informational specificity would be poor but it may reflect the relative motivational state of workers engaged in different social interactions and thus may serve as an additional signal to others to improve their efficiency. However as the authors of the study noted, this subject remains a matter of speculation and stridulation still eludes a satisfactory explanation.

Other forms of communication have been observed in *Leptothorax* but its nature is unclear. Stuart et.al. (1983) reported the initiation of a tandem recruitment in *L. muscorum* that consisted in the scout engaged in a very energetic vibratory pattern involving the entire body and not only the gaster as in stridulation. These motor activities occurred mostly in a vertical plane and were observed to be extremely effective in bringing together the nestmates toward the source. It appears that with this method colonies can be transformed from a calm state to a very vigorous alerted state in a very brief period. However it is not clear if such invitation behaviour involved pheromone release as well or involved sound or vibrational motion propagated through the solid substrate.

1.6 Activity patterns in time

The existence in many groups of insects of particular forms of behaviour that have some degree of regularity through time is well known (e.g. Saunders, 1976 and references therein) and ants are no exception. Rhythmic patterns of specific forms of behaviour in ants exist on different time scales.

Annual rhythms in ant societies exist mainly in correlation with production of sexuate individuals, nuptial flights, mating, colony fission and nest migrations. For a number of species, colony swarms occur mostly in the warm days

of summer. Then annual changes of behaviour are mainly linked with colony seasonal reproductive activity. Some *Leptothorax* are known to hibernate during the winter, announcing the period by a general decrease of activity. There is a reduction of eggs, feeding activities and foraging excursions.

Martin (1991) found in *L. unifasciatus* the existence of a clear annual rhythm in the respiration activity of the colony that proved to be temperature-independent. The maximum of respiratory activity occurred just at the end of the hibernation period and respiratory rates were observed to decay dramatically on October. The author suggested that, since the seasonal cycle was temperature independent, there may be an endogenous mechanism involved. However it should be said that the study did not report control of light-dark periods. It is not clear if the observed "endogenous" mechanism is fixed at the colony or the individual level, since groups of workers isolated from their colonies showed a peak in May while the colony showed the peak in April. This time delay may indicate that a mechanism of social regulation of some sort is present.

Rhythms can occur on time scales of less than a year but larger than a day. A dramatic example of this kind of activity occurs in the raider ant *Eciton burchelli* as first noted by Schneirla (see Hölldobler et.al., 1990 and references therein). In this ant, alternate periods of migration and stationary behaviour over two or three weeks has been observed. It has been possible to correlate these cycles with the reproductive status of the queen. During stationary phase the ovaries of the queen are highly developed and can lay from 100,000 to 300,000 eggs. In a few days these eggs develop and new workers start to emerge. The sudden appearance of thousands of new nestmates trigger an increase in colony activity level and the colony enters a new nomadic phase. This nomadic phase endures as long as the brood belonging to the last stationary phase remains in the larval stage. Once the last larvae eclose, the intensity of the colony decreases and it enters into another stationary phase.

Another time scale is the one for rhythms with periods of 24 hours. *Leptothorax* ants forage at night and are rarely sighted during the day. While not completely understood it is accepted that these behavioural traits are the result of complex ecological and evolutionary processes that link periods of minimal activity of ant's predators and competitors and periods of activity of those organisms that the ant itself predaes. An extreme and illustrative example occurs not in *Leptothorax* but in the desert ant *Cataglyphis bombycina* (Wehner et.al., 1992). This ant forages intensively in very short periods lasting only a few minutes at midday. Foraging activity is restricted to a very narrow outside-nest temperature window of about 46.5–53.6°C. It is thought that *C. bombycina* has developed this particular behaviour to avoid predation by desert lizards that are unable to stand these temperatures and retreat to underground burrows when temperatures approximate the lower threshold of the ant activity window. The upper temperature limit is the maximum the ant can tolerate (this behaviour contrasts with the fact that more than 90% of desert ants forage at night to avoid exposure to intense heat).

Examples of daily rhythms on outside-nest activity are known in some species of harvester ants *Pogonomyrmex*. Ants of this genus seem to switch between

tasks (identified by counting number of workers involved in each category) at characteristic times of day, suggesting well adapted temporal organization (Gordon, 1983; 1984; 1986; 1988 and references therein). In some ants, the 24 hour rhythms have an endogenous nature (circadian rhythms), as is the case of *Veromessor andrei* and *Selenopsis saevissima* males that are active at dawn (Chauvin, 1970, p.179; McCluskey, 1965). It is known that day-night foraging habits in *Leptothorax* are not endogenous. This was reported by Chauvin (1944) in *L. tuberum* var *corticalis*. Martin (1991) did not find, by measuring respiratory rates, any sign of circadian rhythms in *L. unifasciatus* under constant temperature laboratory conditions.

The idea that work performed by ants is an ordered continuous flow of activity is far from being true. Chauvin (1970, p.65), who developed a very ingenious device to measure the intensity of foraging activity in *Formica rufa*, noted that “workers pass [over the foraging trails] in ‘gusts’, as one might say, of 7 to 10 insects, separated by dead periods”.

Inside the nest, it has been realized, for a long time, that not all workers are active at the same time. The proportion of time spent in resting can be high (Sudd, 1967, p.160). However it is not clear why ants devote such a high proportion of time to resting. Outside the nest it may appear that by spending time doing nothing (at least nothing that an observer can identify) they would increase the risks of being predated and, on the other hand, would decrease the efficiency of the foraging expedition. It has been speculated that the reason could be some recuperative physiological function, but the only case known were this argument can be tested is the one present in *C. bombycina* (Whener, et.al., 1992). In this case, the ants appear to be obliged to spend time in refuges in order to dissipate excess body heat, and so periods of inactivity may be linked to a vital physiological function. Nevertheless, for those ants not suffering the extreme conditions of desert heat, it is by no means clear why they spend time resting. Moreover, it is known that ants living under stable laboratory conditions still show the same pattern of behaviour.

This trend of alternate periods of activity and resting was found to exist in *L. curvispinosus* by Wilson et.al. (1974). Unfortunately, these authors failed to recognize that resting may also be a form of behaviour and failed to keep a record of resting times. Latter, Herbers (1983) and Herbers et.al. (1983) working with *L. longispinosus* reported a complete ethogram compiled after 35 hours of observations, with a total of 1562 recorded acts that led them to estimate a behavioural repertoire of 37 separate types classified into four major categories that they named as: personal behaviour, brood care, social interactions and colony maintenance. The frequency distribution found for the four classes is shown in the table 2.2.

While commenting on their findings, the authors of the cited studies wrote: “The total time budget clearly shows that the popular conception of an ant colony being a maelstrom of activity is inaccurate. During our study, ants spent two-thirds of their time apparently doing nothing at all!” and added further that “The strikingly high proportion of time spent motionless was due in part to the absence of contingencies in the laboratory which are important in the field.

In the laboratory, ants had a reliable food source and were free from stresses imposed by competitors, predators and social parasites. Even so, newly-opened nests in the field are populated with many workers at a distance from queens and brood: these ants give every appearance of complete inactivity. It is reasonable to infer then that inactivity prevails within the confines of ant nests in nature. Our study conducted in the height of summer, shows that even when activity should be highest (when alates were emerging, queens were laying eggs and foraging activity was high), workers spent most of their time resting”.

Act ^a	Frequency (%)	number of acts ^b
Personal behaviour	47.7	2
Rest	23.18	
Self-groom	24.46	
Social interactions	25.0	13
Antennate with worker	13.83	
Regurgitate with worker	5.63	
Brood care	24.7	14
Groom larva	8.13	
Inspect larva	7.30	
Colony maintenance	2.6	8
Lick nest wall	0.77	
Handle nest material	0.64	

Table 1.2: Behavioural repertoire for *L. longispinosus*. *a* = only the top two acts are shown for each major category; *b* = number of acts observed in each major category. Data from Herbers et.al., 1983.

Parallel observations and compilation of complete ethograms by Herbers (1983) showed the same basic behavioural trend in *L. ambiguus*. That is, worker’s time was divided mostly in long periods allocated to resting, self-grooming and communication with nestmate workers.

While studying the so called time budgets in *L. allardycei* (Mann), Cole (1986) found the same pattern of active-inactive worker phases and noted that “Time spent quiescent occupies a large fraction of the total time of an ant (on average 55%). When an ant is quiescent it is completely stationary; it does not even move its antennae...quiescence last an average of 17 min and occurs on average 1.9 times per one hour of observation period.”

The same behavioural pattern was found to exist in *L. acervorum* by Franks and Bryant (1987). This time, the authors not only reported the existence of a clear discontinuity in ant colony activity but they were able, by means of ingenious video recording techniques, to keep a record of activity in the whole colony (four colonies were used in this study). The number of active ants

appearing in successive video frames 1 minute apart, totaling 10 hours of filming time were counted (the authors regarded active ants as those that were moving while inactive were those that did not move or that only moved their antennae slightly). Spectral analyses of the time series showed that activity was roughly periodic: periods were found to be 15.6, 16.0, 22.3 and 36 minutes depending on the colony. Also, the authors estimated that workers in this species spent 75% of their time, within the nest, inactive.

After perfection of the observation method, Franks et.al. (1990) reported a more elaborate study that arrived essentially at the same conclusion regarding colony activity in *L. acervorum*. In this study, an experiment was performed to measure the so-called time budget of a randomly selected ant inside an experimental nest partitioned in two sections: the foraging area and the brood chamber area (the nest was kept in between a pair of glass microscope slides). For workers inside the nest, it was found that on average, almost 72% of the time was spent resting, 9% foraging and 9% in undefined movement. The major behaviour observed included antennal contact with workers (3.7%), self-grooming (4.5%) and grooming other workers and larvae (1.8%). Forager workers were active over 85% of the time, compared with only 28% in nestworkers. By using autocorrelation function analyses over the time series, the authors identified periodic cycles in colony activity (only in one of the three analyzed), the period being 15.6 minutes. Further more they revealed that ants tended to remain inactive unless they were activated by an already active ant (see table 2.3). This is in good agreement with the observations made a long time ago by Sudd (1966, p.160): ants can induce movement in stationary ants by disturbing them.

	Remain inactive	Become active
Contacted by another ant	6	15
Not contacted by another ant	22	7

Table 1.3: Pattern of activation by ant-ant contacts. After Franks et.al., (1990)

The first three colonies in the study just mentioned had similar worker populations but otherwise differed in being either monogynous, queenless or polygynous. Nevertheless similarities in the pattern of worker behaviour in each colony were found. In all cases the behaviour of the majority of individuals within each nest was synchronized, so that they tended to be either active or inactive together. This observation demonstrated that queens do not participate in the regulation of colony activity cycles.

This outstanding discovery was made independently by Cole (1991a) in *L. allardycei* as well. In this case, the author experimented with isolated workers, pairs of workers, small groups and whole colonies, making observations based on automatic video recording techniques and regarding activity as proportional to the number of changing pixels, in a computer screen, from frames 30 seconds apart. By applying standard Fourier analysis to the whole colony time series, periodic rhythms of activity with a mean period of about 26 minutes were

detected (range: 15-37). The fundamental question of whether single workers were periodic was resolved: no periodicity was detected, this strongly suggested that activations were occurring spontaneously in an unpredictable way. The same experiment was made for pairs of ants, groups of five and seven ants and the same conclusion reached. But it was noted that “the variation in the interval between movement-activity peaks declines with larger numbers of ants”.

In a subsequent publication, Cole (1991b) analyzed the time series for isolated workers and after measuring the dimension of the reconstructed attractor in the system phase space was able to find a non-integer value strongly indicative of chaos. The conclusion was straightforward: isolated workers activate chaotically!

Hatcher et.al. (1992) reported periodic oscillations in the activity of *L. tubero-interruptus* while Cole (1992) reported them in *L. muscorum* adding another two species to the list of *Leptothorax* that show this pattern of collective behaviour.

1.7 Activity in space

Many different architectural plans and designs are widely used by ants. It includes differences in materials, sizes, preferred sites, etc. Some ants even do not have nests, as in the case of the highly mobile nomadic ants like *Eciton burcellii*. In ants that do have a nest, internal space organization does not follow any common plan and its organization again depends on the species under consideration. Some ants nest in a central and unique chamber while others prefer multiple chambers connected by intricate gallery systems used for different specialized uses. Some chambers (and this is most common in underground nests) are specific for the queen, some for the brood, some for storing food as in harvester species that store seeds in special chambers or the *Myrmecocystus* honey-pot ants that store food in the gaster of specialized workers hanging from the roof of the so called honey chambers, while in some ants the chambers are used for “food processing” like in the case of leaf-cutter *Atta* ants that grow fungus gardens for feeding.

Some ants have specialized chambers for sorting the eggs, larvae and pupae depending on size or age. In those species, workers select the brood and select the correct place for the brood depending on its class. Sometimes the distribution can occur in up to six segregated classes. In this way it is possible that more specialized care can be offered since brood of different ages have different nutritional and environmental requirements (Wheeler, 1960, p.69) This is a very dynamic process that keeps the ants transporting the brood from chamber to chamber continuously following daily changes in temperature and humidity. So workers keep transporting brood near the surface or to more underground places depending on daily weather fluctuations. What appears to be a general characteristic is that in no ant colony is the individual brood kept randomly scattered; they always tend to be kept clustered in groups where workers and queen(s) (if any) usually keep touching, licking or rotating them. In some species, workers

even move the brood outside the nests for brief periods, as in *Ischnomyrmex cockerelli* (Wheeler, 1960, p.69). More dramatic is the fact that the brood is moved when the colony moves from nest to nest or when the colony moves because they lack a fixed nest as in *Aenictus* or *Eciton*.

In one-chamber nests, the brood can be arranged in clusters known as brood pile, a behaviour already known in *Leptothorax* ants. But how is worker activity distributed over the nest and in relation to the brood?. In *L. acervorum*, Franks et.al. (1990) observed that “one such difference was the consistently low activity of the workers closest to and tending the brood, compared with that in the nest as a whole. This was particularly significant as the concentration of ants over the brood was far greater than in the rest of the nest. This suggests that the brood workers and queen(s), which care for the larvae, are less active than the nestworkers, who in turn are much less active than the foragers.”

Cole (1987) reported that in *L. allardycei*, the ants identified as the top ranking because of dominance roles showed a marked tendency to be close to eggs restricting the set of spatial position to those occupied by eggs. This suggested that space distribution of workers and of their activity does not occur randomly, or homogeneously, but there is a tendency for activity clustering.

In *L. unifasciatus*, the brood pile is know to be organized in concentric regions (Franks et.al, 1992). Eggs and microlarvae are at the center and larvae at the periphery. The patterns are constructed by workers who sort the items depending on their age-size conditions and spacing the items in a characteristic way probably linked with metabolic brood requirements. Franks et.al. (1992) have described the richly dynamical process that occurs when the nest of the ant is perturbed and the ant migrates to another nest. The brood transported by the workers is layed in the new nest surface randomly but as new items are brought they are located close to other items belonging to the same class. Those items already within the nest are relocated and the concentric patterns are recreated and the final brood pile formed. *L. unifasciatus* colonies were reported to habit in almost flat surfaces between rock cracks, so that studies on space usage and space activity distribution can be made by observations in laboratory colonies sandwiched between glass slides.

The process of pattern formation was suggested to be self-organized due to the fact that the patterns are recreated even in the absence of the queen (ruling out central control). Self-organization is supported by the observation that if the eggs were simple moved away from the center (occupied by an egg-layering queen), then older items would have to be located in the limiting borders of the cluster. Nevertheless this was not the case because the older items (pre-pupae and pupae) are not located there but in an intermediate position between eggs and the younger larvae. Franks et.al. (1992) suggested a correlation between the relative position, the area around the items and their metabolic requirements.

1.8 Cycles of activity as collective behaviour

As discussed in the introduction to this study, social behaviour is the outcome of the process of interactions among social units. In the case of *Leptothorax* ants it appears quite reasonable, as shown by experiments, to consider the existence of short-period cycles of activity as the result of the process of activation by mutual stimulation of inactive workers. The fact that isolated workers can activate spontaneously indicate that spontaneous activation play a role in breaking the inactive phase of ants and that activity spreads over the nest as active ants move and contact other nestmates. This suggest strongly that the mechanism that is generating the oscillations is very simple and involves the participation of all the ants in the nest, in this sense, oscillations are a global collective behaviour. Now it appears interesting to try to extract just the basic individual behavioural traits of the *Leptothorax* ants and to develop an artificial society based on them. If this approach works we can be confident that periodic oscillations are generic and almost inevitable self-organized properties of interconnected collections of objects. This attempt will be carried out in the next chapter.

Chapter 2

Collective behaviour in artificial systems

From the review made in the previous chapter, some relevant features that strongly characterize the basis of social behaviour in *Leptothorax* ants may be extracted. Those are:

- Classless society (no polymorphism or castes).
- Society not hierarchically organized and without central control or regulation by a single individual.
- Individuals keep very close contact with each other.
- Communications occur mostly by direct short-distance interactions.
- Individuals can change their activity status because of the interactions.
- Isolated individuals can activate spontaneously.

With this list in mind, it is possible to go back to the discussion introduced already in the first chapter where it was argued that social behaviour is best regarded as the result of a synergetic process that arises from a set of individual behaviours. To explore this idea more deeply, I will derive a set of results from the construction of an artificial “social” system. The purpose of this, is to generate a system that can exhibit a wide range of dynamical properties (collective properties) that latter could be compared with the observed behaviour in ants. I consider the system here discussed to be social in the narrow sense of being formed by individual units with individual behaviours that couple to give collective behaviours. I will argue then that some aspects (if not all) of social behaviour are indeed generic and robust collective properties of complex systems (an ant colony being a complex system by implication). The individuals of this artificial “society” may be computer automata, cells, insects, robots or whatever other excitable mobile objects that share the basic six properties

mentioned above for *leptothorax* ants. The model will be based on the notion of *mobile cellular automata* (MCA) (Miramontes et.al., 1993. See appendix B).

2.1 Mobile Cellular Automata

Cellular automata are discrete dynamical systems that consist of a regular lattice of sites. Each site takes on a set of possible values, and is updated in discrete time steps according to fixed rules (Wolfram, 1987). MCA are dynamical systems much like classical cellular automata but with the property that only a subset \mathbf{A} of lattice cells is updated in the time evolution. The elements (objects) that belong to \mathbf{A} are able to move over the lattice. Several authors have used the notion of mobile automata in different contexts: Langton (1986) in simulating properties of an ant farm, Chopard (1990) for the purpose of modelling dynamical properties of solid bodies in lattice spaces, Goss et.al. (1988) and Solé et.al. (1993) used the idea of mobile ant-like objects for modelling *Leptothorax* time cycles of activity, Courtois et.al. (1991) for modelling nest construction in termites, and Boccara et.al. (1992) for the spread of infectious diseases; among others.

A mobile cellular automaton can be defined over a two-dimensional rectangular lattice where a nine-cell-square is considered as the neighborhood where interactions among objects occur. In this way interactions are restricted to short-range first neighborhood distances. The set of cell spaces that belong to this neighborhood will be labeled \mathbf{M} . A collection of n objects, labeled a_i , will be considered as the elements of the set \mathbf{A} :

$$\mathbf{A} = \{a_1, \dots, a_n\}, n \in \mathbf{N} \quad (1)$$

Each object a_i in this 2D lattice is further characterized by four quantities:

$$a_i = \{x_i, y_i, m_i, S_i\} \quad (2)$$

Here x_i and y_i are the two integer space coordinates. New values for x_i and y_i are assigned randomly within \mathbf{M} . The movement pattern is thus essentially a random walk subject to the following two constraints: (i) no two objects will be placed at the same position at the same time, and (ii) new positions will be selected randomly among the lattice cells that belong to \mathbf{M} . If the cell selected as new position is occupied, then the object will look for another one, this procedure being repeated until a free cell is found or after six attempts are made. If no free cell is found the object remains motionless until a next attempt in the next time step (the objects still interact no matter of failed attempts to move, as long as they are active).

A random pattern of movement has been considered here because it represents the most simplified assumption about object's displacements and trajectories and because it is always instructive to see how much dynamic order can arise from initial randomness. This assumption has been used successfully

for many problems in statistical physics where a random walker is commonly referred to as a “drunken ant” or just as an “ant” (Bunde et.al., 1991).

Random activity may occur in the case of ants when foragers are engaged in exploratory activities, but under other circumstances purely random movements are not observed. Organisms are highly sensitive to external stimuli (visual, chemical, auditory, etc.) which can be involved in non-random patterns of movement as in long-term diffusion (Cain, 1991). Also, trail patterns can have fractal dimensions (Fourcassié et.al., 1992), showing that movements outside the nest are directionally biased. However, it may be that trail formation is important not only for increased foraging efficiency but as a way of ensuring that ants can keep in continuous contact, which is essential for their social organization.

The variable m_i in expression (2) is a Heaviside function of a continuous variable S_i :

$$m_i = \begin{cases} 1 & \text{if } S_i > 0 \\ 0 & \text{otherwise} \end{cases} \quad (3)$$

If $m_i = 1$ then the object a_i is regarded as active and may move, otherwise it will be considered as inactive and will remain motionless (both x_i and y_i are updated only if $m_i = 1$).

If the number of objects equals the number of available lattice cells, the system is said to be fully saturated (density=1) and the objects will not move due to the lack of free lattice cells. In this limit condition, a 2D MCA is equivalent to a “classical” 2D cell automaton where all sites in the lattice are updated without motion and where the number and type of connections (the wiring diagram) are invariant throughout the evolution of the system.

Variable S_i represents the object *activity value* and will range continuously from -1 to 1 ($S_i \in \mathbf{R}$). It is calculated by assigning the local field around a_i that is generated by the presence of other objects $a_j \in \mathbf{M}$ and by a_i itself, if self-interaction is considered. The expression for this variable at time $t + 1$ is given by:

$$S_i^{t+1} = \text{Tanh} \left\{ g \left(\left(\sum_{j=1}^k J_{ij} S_j^t \right) + J_{ii} S_i^t \right) \right\} \quad (4)$$

where J_{ij} are coupling coefficients taken from an interaction matrix \mathbf{C} and k is the number of neighbors of a_i . Note that term $J_{ii} S_i^t$ represents the contribution of the self-interaction. \mathbf{C} is the square interaction matrix defined as follows:

$$\mathbf{C} = \begin{pmatrix} c_1 & c_2 \\ c_3 & c_4 \end{pmatrix}$$

whose real-valued entries are selected according to table 3.1.

The parameter g (gain) has been introduced in order to allow the control of the slope of the hyperbolic tangent function. The value of g will determine the rate of activation and deactivation of the mobile objects and its exact role in the dynamics of the model will be discussed later in this chapter.

$S_i > 0$	$S_i \leq 0$	
c_1	c_2	$S_j > 0$
c_3	c_4	$S_j \leq 0$

Table 2.1: Assignment of coupling coefficients in equation (4). c_1 represents active-active interactions, c_3 and c_2 represent active-inactive and inactive-active interactions, while c_4 represents inactive-inactive interactions. The sign of the i and j elements are considered together. For instance, if $S_i > 0$ and $S_j > 0$ then the interaction is of the active-active type and $J_{ij} = c_1$.

The motivation for the use of the hyperbolic tangent function is, that it has two features that make it ideal in models that involve biological excitable units (neurons, ants, etc.). First, the function is bounded in the interval $[-1, 1]$ and because of this, it never grows up to infinite when iterated. Hence, a given excitable element never goes towards a state of infinite excitation. Second, the rate of change in the excitation can be controlled with only one parameter: the gain. This parameter determines if the function grows towards the extremes of the interval or towards the zero, being those three the only attractors of the iteration process.

Without any external input (no interactions) an isolated inactive object will remain so unless it is randomly activated by assigning a non zero value to S_i^t . This value will be labeled s_a (*spontaneous activity level*). This process of random activation takes place only if $r > p_a$, where $r \in [0, 1]$ is a random variable and $p_a \geq 0$ represents a probability value threshold (*probability of spontaneous activation*).

2.2 System microdynamics

Consider the case of a single isolated object on a lattice (only self-interacting objects will be examined here). The value of the gain is fundamental for the dynamics of the system. For $g > 1$, the limit behaviour of the variable S_i^t is a positive constant that approaches the value 1 as g is increased. For values of $g \leq 1$, the limit attractor is the value zero. Thus a self-interacting process modelled in a digital computer, with $g \leq 1$, will attain a zero value of activity after a finite number of time steps.

Consider figure 3.1 where the graph of the sum $S_1^t + S_2^t$ (total activity) of two interacting objects in a small lattice is shown. Because of the existence of interactions total activity is not globally monotonically decreasing to zero, rather, we can see the existence of peaks where interactions occur that signals an increase in the total activity and the interchange of activity among the pairs of objects. In the intervals where no interactions occur the curve is monotonically decreasing as expected.

When mobile elements do not interact they tend to freeze because of the impossibility of activity interchange among them. When random activation is

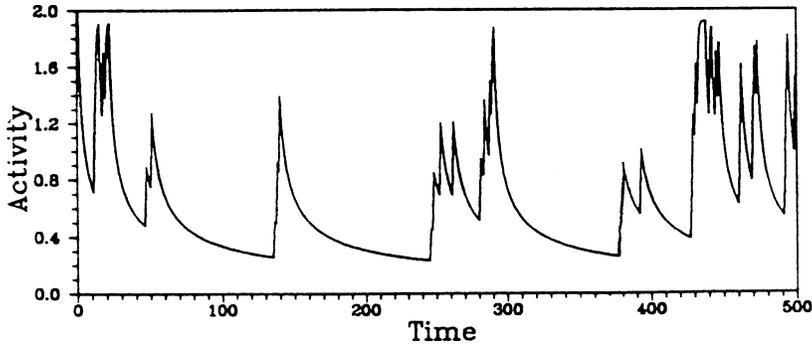


Figure 2.1: Dynamics of the total activity in MCA with two interacting objects. The zero attractor is never reached because activity is increased with each interaction. Lattice size 10×10 , $g = 1$, matrix coefficients all one. Initial activity value = 1 for both objects.

not permitted, it is possible to provoke the freezing of any arbitrary number of mobile objects, if the lattice size is large enough so as to make the mean time for an interaction to occur larger than the time needed for the individual activity to decrease to zero. If these conditions hold the objects are, on average, isolated. Another way to provoke the freezing of the system is to make the time needed for decrease to zero shorter than the mean interaction time, specially if the lattice size is not very large. This is accomplished by setting the value of the gain parameter to an adequate value (usually a value $\ll 1$). Quite the opposite, if one desires to prevent the system from attaining the zero state value, the gain can be adjusted for this purpose (usually a value ≈ 1).

The mean time for an interaction to occur in a square lattice of size l with two objects on it is given by a power law distribution. This is a very well known result from the theory of interacting random particles as, for instance, the problem of encounters between random predators and random prey (see: Durrett et.al., 1991). This mean time can be expressed as :

$$\langle m \rangle = l^\alpha + \beta ; l \geq 2 \quad (5)$$

It is possible to further characterize the dynamics of the activity value for a system of two interacting objects. In fact, after measuring the Lyapunov exponents of a series of times like the one shown in figure 3.1, one finds that the dynamics of interactions between the two objects is chaotic as suggested by the positive signs of the Lyapunov exponents (Wolf et.al, (1985) algorithm was used to calculate exponent values). A Lyapunov spectrum for different values of g is shown in fig 3.2. As can be seen, the gain works as a “bifurcation-like” parameter and chaos is first detected for values of $g \approx 0.5$. For the system parameters used, this value of g corresponds to the value for which the mean

interaction time between the two objects is just greater than the time for the activity to decay to zero, thus the system is self-sustained and chaotic.

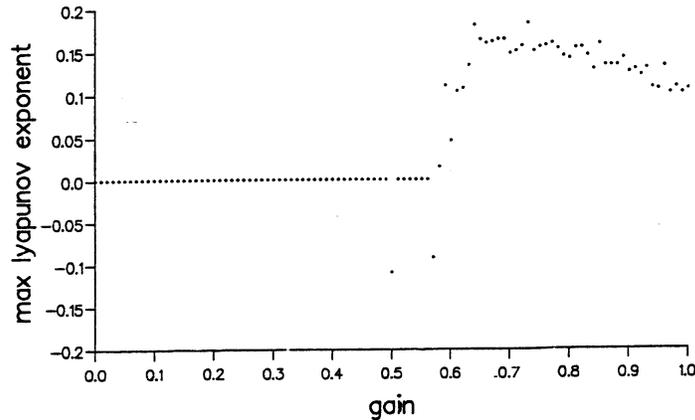


Figure 2.2: Lyapunov spectrum for the dynamics of the total activity in a system with two interacting objects. Note the transition to positive exponent values at $g \approx 0.57$. Lattice size 6x6, matrix coefficients all one. Initial activity value = 1 for both objects

It is usual to expect the presence of chaos for systems with three or more interacting objects as was first identified a long time ago by Poincaré, in the study of the many-body problem in classical mechanics (eg Crutchfield et.al., 1986). Recently, a number of systems with only two particles have been identified as exhibiting chaotic motion. One of them is the case of two ions trapped in an electromagnetic field (Brewer et.al., 1991). The phenomenon found here, of chaos in two interacting random-walkers with activity given by equation (4) is new, although the presence of chaos in this system was first reported for the case of four particles (Miramontes et.al., 1993. See appendix B).

2.3 The dynamics of social facilitation

The fact that self-sustained phenomena can exist in a system of interacting objects implies that the average activity of the system is increased by the process of interaction. Such systems can have properties that are “more than the sum of the parts”, a well known and widely used expression applied to synergetic non-linear collective phenomena. In connection with this, one of the most interesting aspects of social behaviour is the fact that interactions between social units can initiate or magnify certain behavioural traits not present or weakly present when the social units are isolated, a phenomenon known as social facilitation (eg. Klotz, 1986). Social facilitation is present in many groups of social and semisocial organisms. It is known to exist in cockroaches that eat more

and grow larger if kept in groups than if held separate. The same occurs in many other organisms including humans (DeCastro et.al., 1992 and references therein). In ants, the existence of this phenomenon was noted by Chen (1937) who experimented with the digging activity of *Camponotus japonicus*. His results indicated that isolated workers performed poorly in digging activities in comparison with groups of ants. The ants in groups dug more and faster (for a critique to Chen's work see Sudd,1967, p.163). The same results on social facilitation phenomena were identified in *Formica subsericea* digging ants by Klotz (1986).

As an artificial "social" system we can ask what kind of social facilitation, if any, is present in mobile cellular automata. Consider the graph shown in figure 3.3. Here, the total activity value of two interacting objects is represented as a function of the gain. As can be seen, there exists a value of g for which the graph shows a phase transition. This is the value for which the mean interaction time is just greater than the time for the activity of an isolated object to decrease to zero. For values of g between 1 and approximately 0.5 the activity value decreases monotonically. Over this range, the objects are active all the time. In the range less than 0.5, random activation and activation caused by interactions exist. There, the value of the activity is almost constant (the graph scale is log-linear) and in fact greater than the activity at lower values of g where the objects become active all the time. This difference in behaviour is also correlated with the finding of a transition to chaos as previously discussed.

Perhaps, the best way to demonstrate the existence of social facilitation is not to look at the activity value directly but to look at the times a given collection of objects have been active. Then it is possible to compare a MCA with only one object with a MCA with two objects, the g can be varied and the quotient between the number of times the objects have been active can be calculated for each g value. If the system were linear, such a quotient would be two, so that the activity of two objects could be regarded as the direct sum of two objects considered apart (this is the well known superposition principle). The result of this experiment is shown in figure 3.4. As can be easily seen, there exists a range of values of g where the quotient is greater than two. In fact the only range of g values where it is exactly two, corresponds to the values for which the objects are all the time active. So the process of activation (by mutual interactions) and further deactivation is the ultimate cause of the synergetics of social facilitation in this model.

2.4 System macrodynamics

Once it is clear that the process of interactions are the source of non-linear dynamical behaviour, we can ask how the system performs for a large number of objects, let's say 100, the number of individuals found in a typical *Leptothorax* colony. For this, consider the series of graphs that appear in figure 3.5 showing the time evolution of a number of active objects in a given system (lattice size 10x10, $g=0.05$, $s_a=0.01$, $p_a=0.01$, coupling coefficients all one, initial values of

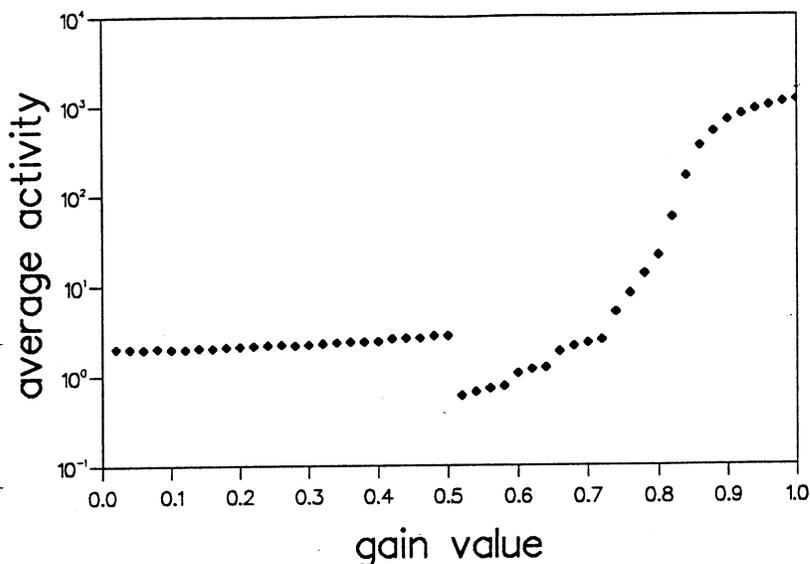


Figure 2.3: Average activity value in a two objects system. Each dot represents the average value of 100 separate time series each 1000 time steps long. Lattice size 5x5, matrix coefficients all one, $p_a=0.01$, $s_a=0.1$. Ordinate axis is logarithmic.

S_i^t were assigned randomly in the interval $[-1,1]$ and initial positions were chosen randomly as well).

In graph (a), the temporal evolution of the system containing just one object is represented. As expected, the occurrence of the peaks showing when the object is active are distributed randomly. In (b) the same situation is represented but with 20 objects. Subsequent graphs are for 40 objects (c), 80 objects (d) and 100 objects (e).

Analysis of these graphs permits us to identify a very interesting phenomenon in relation to the system density (defined as the number of objects divided by the number of lattice cells). In particular, it is possible to observe the emergence of well defined oscillations in the range of medium densities, while in the range of higher densities the periodic nature of the oscillations is evident. In contrast, in the range of lower densities, no periodic behaviour in the temporal evolution is present at all.

The relationship between the period of the oscillations and the system density was explored using standard Fourier analyses and it was found, as depicted in figure 3.6, that this relationship has two components. For density values of about 20% and more, the relation is almost linear and has a tendency to increase slightly as the density is increased until reaching the top value of 36.6

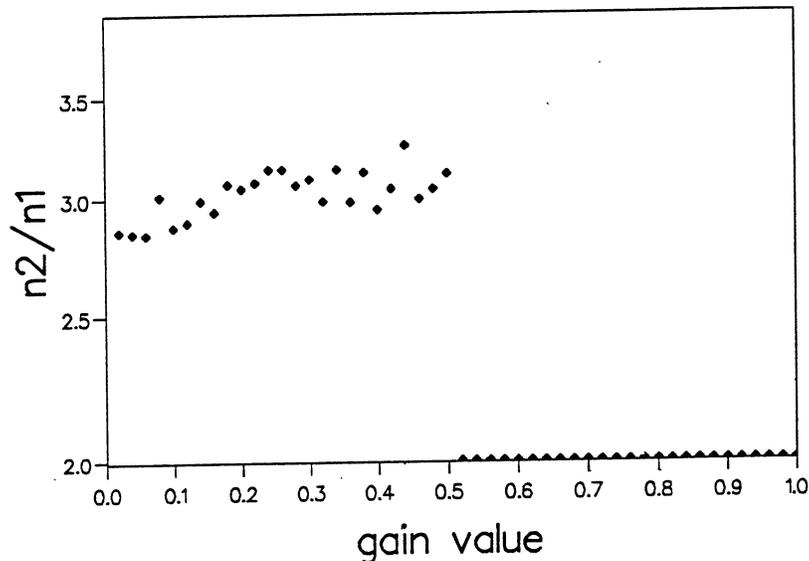


Figure 2.4: The quotient between total number of active objects in a system of two objects (n_2) and a system of one object (n_1) is shown as a function of the gain. Each dot represents the average value of 100 separate time series each 1000 time steps long. Lattice size 5×5 , matrix coefficients all one, $p_a=0.01$, $s_a=0.1$.

for the combination of parameters used. For values of density less than 20%, the number of interactions between the objects is so low that periodic synchronization starts to disappear. For even lower values of density, the period length apparently increases and can be described by an exponential function. However in this region, the periodic behaviour is almost lost so that Fourier analysis reveals only very weak periodicity.

2.5 Stability and robustness

As stated before, the gain controls the rate of deactivation of an isolated object and the activation rate of an interacting object. If g is made to have a large value (usually $g > 1$), S_i^t will flip-flop between values 1 and -1 or 1 and 0 if only positive values are permitted. Under these circumstances the system approaches the discrete binary limit. Gain g also has a very important role in determining the period of the collective oscillations. As a general trend, the period is incremented with increments in g . Nevertheless this trend is broken because, as stated, a large value for g will make the system approach the discrete limit and if this happens periodic behaviour is lost.

Probability p_a has the overall effect of increasing the number of active objects

but does not have an important role in determining the period of the oscillations, once oscillations are observed.

Coupling coefficients in matrix \mathbf{C} play an important role. It is possible to regard equation (4) as a weighted process since these coefficients “weight” the relative importance of the objects in the interaction. Coupling coefficients may be interpreted as weights for the three types of interactions (active-active, inactive-active and inactive-inactive).

In order to explore the behaviour of the system as a function of the matrix values, I will consider first the most simple matrix structure. Suppose the entries of \mathbf{C} are binary, that is $\mathbf{C} \in \{0, 1\}$. Also, suppose that s_a is always a positive quantity so that, after an initial transition, the values of S_i^t will be always positive for all active objects and zero for the inactive ones. Let us now divide the analysis into several particular cases:

a) Suppose all S_j^t objects that interact with an active S_i^t at a given t are active. Then: $S_i^t > 0$ and $S_j^t > 0$. Interactions between active-active objects are weighted by coefficient c_1 , then equation (4) can be rewritten as:

$$S_i^{t+1} = \text{Tanh} \left\{ g c_1 \left(\left(\sum_{j=1}^k S_j^t \right) + S_i^t \right) \right\} \quad (6)$$

Depending on the value of c_1 we have two further cases:

i) $c_1 = 1$. Here, the expression is only a function of g and depending on its value, S_i^{t+1} could be greater, less than or equal to S_i^t . In the case when $S_i^{t+1} < S_i^t$ the object deactivates after a finite number of time steps. In the other two cases, the object stays active all the time.

ii) $c_1 = 0$. In this case equation (6) is equal to zero, that is: $S_i^{t+1} = 0$ and an initially active object deactivates after just one time step.

b) Suppose all S_j^t objects that interact with an active S_i^t at a given t are inactive. Then $S_i^t > 0$ and $S_j^t = 0$ and equation (5) can be rewritten as:

$$S_i^{t+1} = \text{Tanh} \left\{ g \left(\left(\sum_{j=1}^k J_{ij}(0) \right) + J_{ii} S_i^t \right) \right\} \quad (7)$$

Since $J_{ii} = c_1$ this last expression reduces to:

$$S_i^{t+1} = \text{Tanh} \left\{ g c_1 S_i^t \right\} \quad (8)$$

Here again we have two cases that depend only on the values of g and c_1 and are identical to the situation discussed for case **a)**, except that here the only term is the one that correspond to self-interaction. In other words there are no interactions between objects.

c) Suppose all S_j^t objects that interact with an inactive S_i^t at a given t are active. Then $S_i^t = 0$ and $S_j^t > 0$. Here interaction between inactive-active objects are weighted by coefficient c_2 and equation (4) can be rewritten as:

$$S_i^{t+1} = \text{Tanh} \left\{ g c_2 \sum_{j=1}^k S_j^t \right\} \quad (9)$$

Here two cases exist depending of the value of c_2 and again are equivalent to the case discussed in **a**).

d) Suppose all objects are inactive. Then $S_i^t = 0$ and $S_j^t = 0$. Here equation (4) has all components equal to zero and $S_i^{t+1} = 0$ all the time.

After this brief qualitative discussion it is possible to note that only matrix coefficients c_1 and c_2 are involved in defining the dynamics of the system. The matrix being binary, implies that only four distinct qualitative behaviours can be expected to exist. In this case, the matrix obviously reduces to a two component binary vector. The four behaviours are shown in figure 3.7 and correspond to the classification shown in table 3.2.

Class	c_1	c_2	Behaviour
I	0	0	Random
II	0	1	Quasiperiodic
III	1	0	Long-periodic
IV	1	1	Short-periodic

Table 2.2: Classification of the dynamical behaviours present in the MCA model

Only the short-periodic behaviour is robust in the sense that its qualitative periodic behaviour is conserved after drastic variation in the number of interacting objects. In class III, periodicity occurs only for large density values (period length was found to be in the range between 250 and 300).

It is interesting to compare the phenomenology present for class III and class IV behaviours. In class IV the objects interact among each other no matter what their activity status: active objects interact with other active ones and can activate inactive objects when in contact with them. On the other hand, in class III, only active objects interact and they do not activate inactive ones, they just “ignore” them. From the point of view of social facilitation it is clear that class III objects are very inefficient in propagating activity, while class IV maximize social facilitation, a result consistent with the robustness exhibited by them.

Now, we can relax the condition imposed on the matrix entries and consider them to be real valued in the interval $[0,1]$. Again and by means of extensive computer simulations, the only four different behaviours found are the ones discussed above. By allowing the continuous variation of the entry values one finds that for a very large range of matrix values, the dominant behaviour is class IV. There is a transition to class III only when the value of c_2 is very close to zero, in the order of 1×10^{-6} and the same happens in the transition from class IV to class II when c_1 is in the same magnitude close to zero. Also there is a transition to class I when both c_1 and c_2 are very close to zero.

What is evident is that if we consider the values of the matrix to be subject to noise and fluctuations (a common situation found in natural systems), the existence of all classes except class IV is expected to be very rare so that these behaviours are very unstable. An immediate consequence is that we could expect to find short-period oscillatory behaviour in almost all systems that share the six behavioural features in *Leptothorax* ants. This must be true, presumably, for several more ant species from different genera and, perhaps, for other insects as well.

2.6 Space dynamics

A MCA is an excitable medium with the property of supporting the propagation of pulses of excitation due to the ability to activate collectively following a perturbation of the resting-inactive state. Since a MCA involves mobile elements, the excitable medium is of a very special sort and is best regarded as an excitable fluid: objects move and excite each other like particles in a fluid.

Because of this property of fluidity, we can not expect to find fixed long-term spatial structures in the lattice, but in order to explore what kind of accumulated behaviour exists in the space domain, it is possible to count the number of times a given lattice cell has been active. First of all, we can explore what consequence it has for the spatial distribution of activity the existence of activity propagation by means of interactions, as will be done in the following example.

Consider figure 3.8 where two MCA systems with 80 objects each are represented. In the series (a), the objects do not interact, they simple move randomly when active and stop when inactive. The equation governing this behaviour is given by:

$$S_i^{t+1} = \text{Tanh} \left\{ gc_1 S_i^t \right\} \quad (10)$$

Frames show the time evolution at four different times. The space distribution (accumulated activity) is simply a random pattern that evolves without any order.

Series (b) shows a system where the objects all interact. It corresponds to the system described in figure 3.5. In this case, there is a clear trend towards the formation of clustering structures where greater activity is concentrated at the centre of the region. A first conclusion is immediate: only systems with mutually interacting objects are able to generate some degree of spatial order.

The finding of a region with greater activity is consistent with another simulation in which the sites where random activation occurred were mapped. In this case random activation was found to be mostly confined to the periphery of the lattice. Since no initial information was given on where greater activity should occur, it appears appropriate to consider the existence of such patterns as the result of a self-organized phenomenon caused by the mechanics of interactions.

Miramontes et.al. (1993. See appendix B) explored the dynamics of spatial distribution of activity for the case of saturated lattices and found that under such conditions, only matrices that produced oscillations in the time domain were found to produce concentric patterns in space. Class IV rapidly produces well defined concentric regions of activity that, however, disappear when mobility is introduced at density values of about 0.8. Class III behaviour produces very distorted concentric regions of activity and is unstable to mobility. In fact, both concentric rings and oscillatory behaviour are lost as density is lowered even if density is high in comparison with those density values that cause loss of collective behaviour in class IV. This is consistent with what was said about the non-robustness of this behavioural class.

Further, the relationship between spatial order and lattice size was explored and it was found that clustering in a single region of greater activity is lost as lattice size is increased. For instance, a lattice 20x20 with 400 objects was found unable to exhibit concentric rings of activity. Instead, four different small regions of greater activity were produced at the corners of the lattice space. This suggests that a system based on short-range nearest neighborhood interactions is unable to maintain coordination of all elements if the system is large, as was pointed out by Gallas et.al. (1992) in deterministic cellular automata with noisy collective behaviours. In the context of *Leptothorax* ants, this result may suggest that a maximum number of colony members may exist before colony coordination loss can lead to colony fission. This result is also in good agreement with the suggestion made by Hölldobler and Wilson (1991) that increased diversity and complexity of communication is correlated with increased colony size.

Existence of self-organized space patterns may be relevant due to the fact that little or no encoding about space usage has to be previously stored in the individual interacting mobile objects: global spatial distribution of activity can emerge from the process of local interactions only.

2.7 Ants and MCA

As discussed in chapter 2, *Leptothorax* ants exhibit collective oscillations in the nest activity that is produced by worker interactions. Also, some degree of spatial activity clustering occurs in their nest surface associated with the presence of a brood.

A number of models have been presented to attempt the simulation of periodic oscillations in *Leptothorax* (Goss, et.al., 1988; Hemerick et.al., 1990; Tofts, et.al.,1992; Solé et.al., 1993)). All of them differ markedly in the assumption of the origin of the cycles and in their degrees of biological realism and predictive ability (see Tofts, et.al. (1992) for a review of most of them). The model by Solé et.al. (1993) is very close to the one discussed here, however in that model the notion of MCA is not used at all but instead the term neural automaton was preferred. The reason for this is that in doing so, the doors are left open for future work that can attempt to link with neural network theory in order

to reconstruct the metaphor of ant colonies as brain-like structures and thus can permit speculations on collective computational capabilities of ant societies (like collective memory and learning). Also there are some differences worth mentioning. In Solé et.al. (1992), interactions occur only among pairs of ants and not with all in the first neighborhood. Also some degree of interindividual variability was introduced by allowing g to have a range of values rather than a single one for all the objects. Finally the process of activation was also simulated with a deterministic chaotic map. Despite those differences the results are in good agreement with those reported here for MCA. This is further strong evidence that, indeed, collective behaviour in mobile interacting systems is very robust.

In my opinion, the notion of interacting mobile automata is very valuable for the exploration of the collective spatiotemporal behaviours exhibited by ants. If we can show the emergence of comparable collective behaviour in natural and artificial systems that share the same class of behaviours at the individual level, we can be confident that such social behaviour are synergetic properties of these societies. Societies, in turn, are self-organized complex systems.

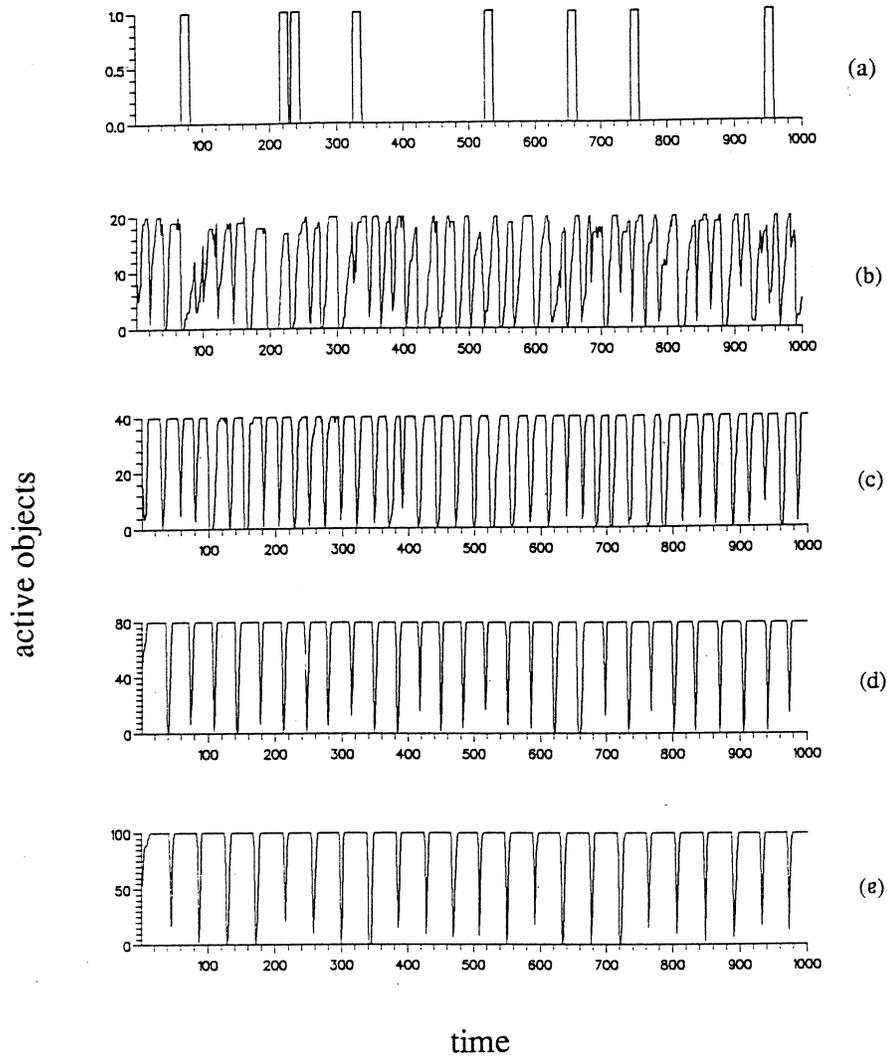


Figure 2.5: Emergence of collective oscillations as a function of density. These oscillations are the result of interactions and can be considered to arise from a social facilitation mechanism. The patterns of oscillations may appear to be different to those that have been found to exist in ant colonies. Nevertheless it is important to notice that the patterns that match those found experimentally are the ones with low density (typically around 0.2) and this seems to be the natural density value in nests. In fact, the time budgets for the objects in the model are similar to those found in real colonies, with around 50 per cent, or more, of the time spent motionless. Also, it is important to keep in mind that activity here means absolute number of mobile objects rather than number of changing pixel on videotaopes. See text for system parameters.

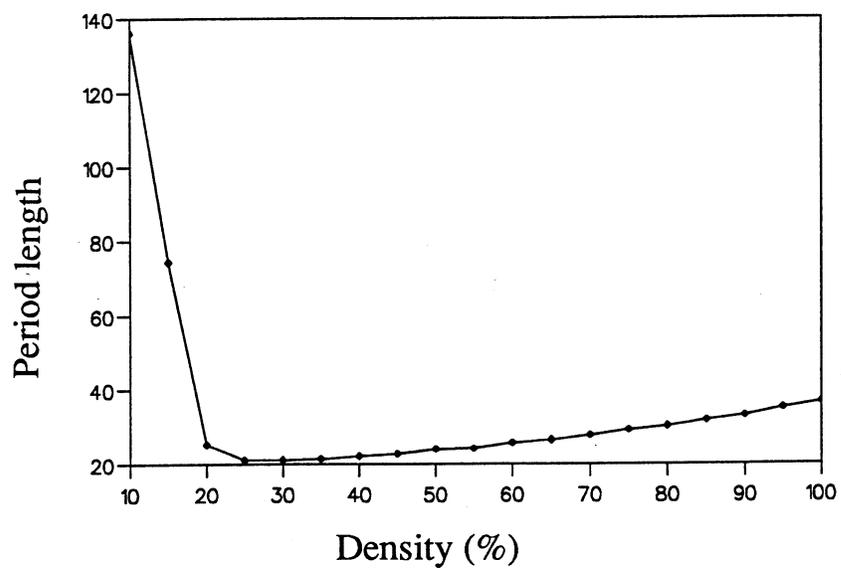


Figure 2.6: Period length as function of system density. Each dot is the average value of five different time series 1024 time steps long. Period value is the peak value of the power spectrum determined by means of a standard fast Fourier transform. System parameters are the same as in figure 3.5.

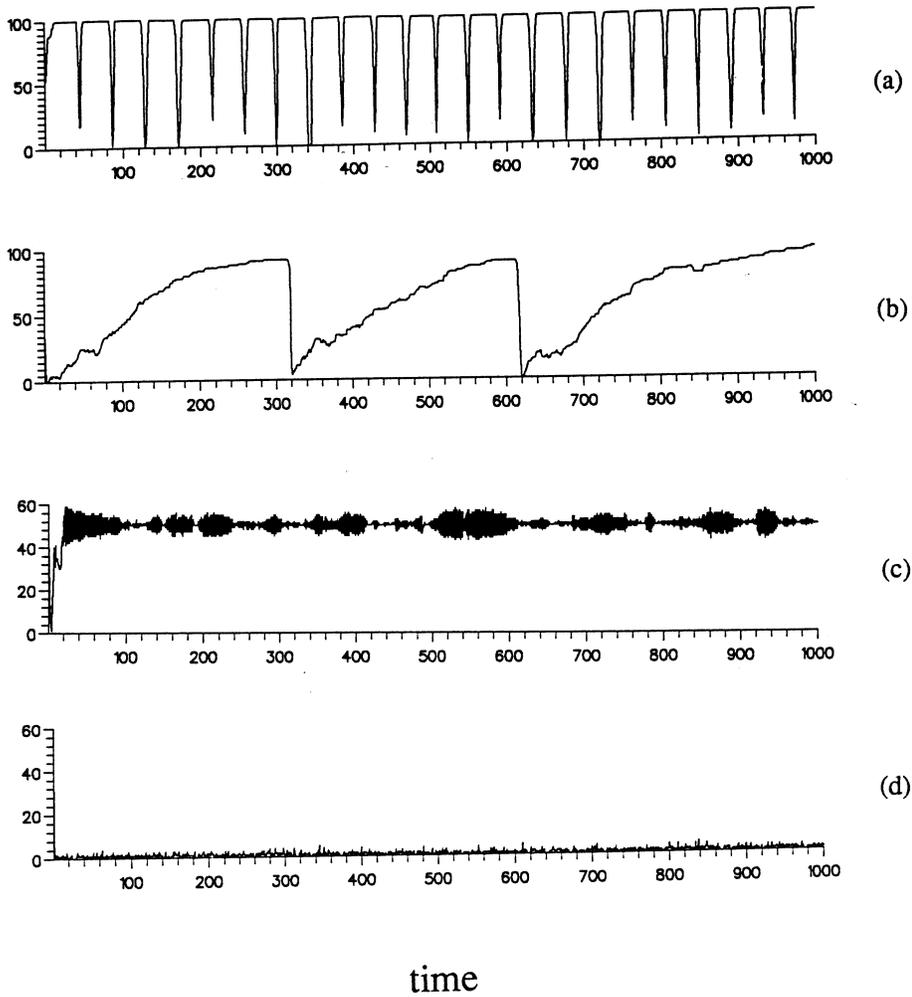


Figure 2.7: Four dynamical behaviours present in the MCA model with binary matrix and $s_a > 0$. (a) $c_1=c_2=1$ (class I); (b) $c_1=1, c_2=0$ (class II); (c) $c_1=0, c_2=1$ (class III) and (d) $c_1=c_2=0$ (class IV). $c_3=c_4=1$ in all cases.

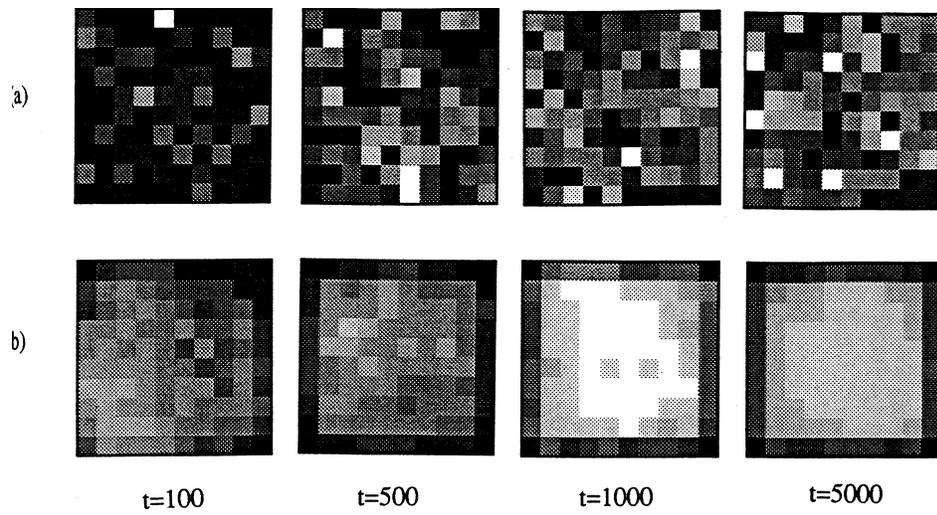


Figure 2.8: Time evolution of space organization for two MCA systems. (a) represent the case of a system with non interacting elements. (b) represents the case of interacting elements with matrix coefficients all one. In both cases: Lattice size 10×10 , number of objects=80, $p_a=0.01$, $s_a=0.1$, $g=0.05$. Time steps are shown

Chapter 3

Summary and discussion

Understanding insect's social behaviour as generated by interactions between individuals is one of the current challenges in biology. It seems appropriate to regard insect societies as highly ordered structures resulting from self-organized mechanisms whose ultimate explanation is the existence of several densely connected discrete elements that are able to modify their individual behaviours in response to the presence of others elements. Social behaviour being a collective phenomenon is, probably, a generic and almost inevitable property of connected complex systems.

The study of collective behaviour in non-linear dynamical systems is one of the most successfully attempts to explain the origin of the so called synergetic phenomena that do not obey the superposition principle, in short, phenomena in which the measured observables are “more than the sum of their parts”. Obviously, social behaviour belongs to this category and it is very instructive to develop computer models of connected elements that are able to show very similar behaviour to those exhibited by real biological organisms. This approach has been recently explored in ants and the present work is part of this trend. In particular, it seems that some of the behavioural traits present in *Leptothorax* ants are quite adequate for this.

Leptothorax ants belong to the subfamily Myrmicinae and to the family Formicidae. These are worldwide distributed ants, very small in size and with colony sizes of around 100 individuals. They are often described as very compact and living in close proximity to each other. Natural colonies can occur without a queen or with multiple queens suggesting that a queen is not essential for controlling the life of the colony. Several communication methods are in use by these ants but it appears that antennation is one of the most important in normal inside nest information exchange. Since antennation is short-range, *Leptothorax* ants tend to live closely.

The temporal pattern of activity inside a *Leptothorax* nest is not uniform since the ants spend most of their time resting. Moreover, activity is not constant but has a characteristic pattern of periodic oscillations. This phenomenon has been identified on at least four different species. Experiments have shown

that individual ants are not periodic but can activate spontaneously in a fashion that appears to be chaotic. Two individuals kept together can interact and activate the other if the other is inactive. This produces increased activity similar to a social facilitation mechanism. More ants together are able to synchronize through interactions and to exhibit periodic collective oscillations despite the fact that the individual's behaviour is not periodic at all.

It appears that periodic collective behaviour in *Leptothorax* is a self-organized process originated in the interactions of the individual ants. This behaviour is robust in the sense that it is "fault-tolerant" in respect to the number of individuals, that is, oscillations do not depend on a critical number of individuals and are sustained over a wide range in the number of ants.

Activity in the nest space appears to be non-uniform and some degree of clustering exist in correlation with the brood pile. This indicates that inside the nest there are portions of the space that are visited most.

The study of artificial societies is one of the current subjects of the so called Artificial Life, a new research field comprising computer sciences and theoretical biology. Artificial social systems can be defined as those that are integrated by several discrete autonomous elementary objects that are able to interact and modify internal variables as a consequence of the interactions. Those systems are quite capable of displaying collective robust behaviour. In this work I have presented a model based in the individual behavioural traits of *Leptothorax* ants. This model exhibits a range of self-organized behaviours that resemble closely those of the real ants. Since no details were given about internal organization or about purpose-oriented behaviour (such as energy optimization, etc.) it seems adequate to regard those collective behaviours as being generic properties of densely connected systems.

The formalism used in this work has been named Mobile Cellular Automata. It consist of a number of objects on a lattice that are able to move and to interact by means of direct contacts. Interactions modify the internal variables of the automata. Each automaton is able to activate spontaneously and to be activated if contacted by another active one. This collection of automata is able to exhibit robust collective periodic oscillations and to show some degree of spatial order.

In biology, it is common to attempt to explain all phenomena in terms of adaptive advantages. However, in the case of periodic cycles in *Leptothorax* ants the adaptive advantages are not clear. It has been suggested that alternate periods of activity and quiescence can limit energy expenditure and colony resource wastage or that they can serve to reduce task repetition thus increasing colony efficiency (Hatcher et.al., 1992). Other authors suggest that those cycles may not be themselves adaptive but that are the inevitable outcome of interactions (Cole, 1991b), a situation already suggested for other kinds of biological rhythms as well (Kauffman, 1986). One outcome of this process of interactions may be periodic oscillations but other dynamical behaviours may be present depending on the strength of couplings and on the details of the spontaneous activations (a phenomenon already observed in the MCA model). This problem is related with the challenge already mentioned in the introduction to this study, that is, the problem of explaining social behaviour in terms of individual behaviours. A

problem that involves the integration of different levels of complexity where the mechanisms of selection are far from being clear. Understanding the generic collective properties of computer models of autonomous agents may give answers to many aspects of this important problem.

Appendix A

This appendix contains the computer program list developed in language Pascal for the simulation of the MCA.

```
Program object(Input, Output, ac, esp);
```

```
{-----  
OBJECT.PAS
```

```
This program is a Pascal version for the VAX-VMS compiler. It contains  
standard Pascal instructions and can be easily transported to other  
computers environments.
```

```
The program simulates a system of MCA (Miramontes et.al., 1992)
```

```
Octavio Miramontes (c)  
Open University, Biology  
Milton Keynes MK7 6AA
```

```
Creation date: 01/08/91  
Last modification: 02/05/92
```

```
-----}
```

```
Const
```

```
maxxmu = 11;  
maxymu = 11;  
conact = 0.1;  
g_range = 0;
```

```
{ maxxmu and maxymu are the maximum X-Y lattice lengths. These values }  
{ are always one unit greater than the real lattice. Thus a 10x10 }  
{ lattice requires setting those variables to 11. }  
{ conact is the activity value for each object after random activation}  
{ g_range is the range value for allowing inter-object variability in }  
{ the gain. A value of 0 means all objects have the same g value. This}  
{ variable only can have values in [0,g) }
```

```
Type
```

```
vector =  
Record
```

```

    x, y : Integer;
    e, g : double;
End;

```

```

{ vector is a defined record who will be used to represent each object }
{ [].x and [].y are the lattice positions. [].e is the value of         }
{ activity and [].g is the value of the gain                           }

```

Var

```

object : Array[1..10] Of vector;
numit, num, maxx, maxy, maxit, seed : Integer;
i, j, k, movx, movy, : Integer;
ran, suma, suma2, g, pac : double;
ac, esp : Text;
grid : Array[0..maxxmu, 0..maxymu] Of double;
es : Array[1..10, 1..10] Of Integer;
nact, aai : Array[1..50000] Of double;
wij : Array[1..2, 1..2] Of double;
newstate : Array[1..10] Of double;

```

```

{ object: the array that contains the maximum number of objects }
{ numit : number of iterations; num : number of objects         }
{ maxx and maxy : lattice lengths; maxit : maximum number of   }
{ iterations; seed : initial value for the random number genera- }
{ tor; movx,movy: unit random increments for new positions      }
{ suma, suma2 : number of active objects and total sumed value  }
{ of activity in each time step; g : gain; pac : threshold value }
{ for random activations; ac : output file containing number of }
{ active objects at each time step. esp : output file for acumu- }
{ lated values of activity over the lattice; grid : the actual  }
{ lattice; es : array for storing acumulate values of activity  }
{ over the grid; nact, aai : arrays for storing the values of   }
{ number of active objects and total activity for each time step }
{ wij: the interaction matrix; newstate : pass array used for   }
{ temporal storing of new active status for each object        }
{ In the variable setting show the system has 10 objects in a  }
{ 10x10 lattice and will evolve with a maximum of 50000        }
{ time steps                                                    }

```

```

Function mth$random(Var seed : Integer) : double; External ;

```

```

{ mth$random is the external VMS random number generator. The RNG }
{ generates numbers in (0,1) using the linear congruential method. }

```

```

{----- Definition of the htan function -----}

Function Htan(Var u : double) : double;
Var ep : double;
Begin
  u := u*object[i].g;
  ep := Exp(2*u);
  Htan := (ep-1)/(ep+1);
End;

{----- Initialization procedure -----}
Procedure inicia;
Begin
  For i := 0 To maxxmu Do
    For j := 0 To maxymu Do
      grid[i, j] := -2.0;
  For i := 1 To maxx Do
    For j := 1 To maxy Do
      es[i, j] := 0;
  For i := 1 To num Do Begin
    Repeat
      ran := mth$random(seed);
      object[i].x := Trunc(Ran*maxx)+1;
      ran := mth$random(seed);
      object[i].y := Trunc(Ran*maxy)+1
    Until grid[object[i].x, object[i].y] = -2.0;
    ran := mth$random(seed);
    If ran <= 0.5 Then
      object[i].e := mth$random(seed)
    Else
      object[i].e := -mth$random(seed);
    grid[object[i].x, object[i].y] := object[i].e;
    object[i].g := g+(g_range*((2*mth$random(seed))-1));
  End
End;
                                     { inicia }

{----- Movement of active objects -----}
Procedure mueve(i : Integer);
Begin
  If object[i].e > 0 Then Begin
    j := 0;
    Repeat

```

```

j := j+1;
Repeat
  ran := mth$random(seed);
  movx := Trunc(ran*3)-1;
Until (object[i].x+movx > 0) And (object[i].x+movx <= maxx);
Repeat
  ran := mth$random(seed);
  movy := Trunc(ran*3)-1;
Until (object[i].y+movy > 0) And (object[i].y+movy <= maxy)
Until (grid[object[i].x+movx, object[i].y+movy] = -2.0) Or (j = 6);
If j < 6 Then Begin
  grid[object[i].x, object[i].y] := -2.0;
  object[i].x := object[i].x+movx;
  object[i].y := object[i].y+movy;
  grid[object[i].x, object[i].y] := object[i].e
End
End
End;
                                { mueve }

{----- Local field computation -----}
Procedure calcampo(i : Integer);
Var
  coorx, coory, c, r : Integer;
  field : double;
Begin
  coorx := object[i].x;
  coory := object[i].y;
  field := 0;
  If grid[coorx, coory] > 0 Then
    c := 1;
  If grid[coorx, coory] <= 0 Then
    c := 2;
  For j := (coorx-1) To (coorx+1) Do
    For k := (coory-1) To (coory+1) Do
      If grid[j, k] >= -1 Then Begin
        If grid[j, k] > 0 Then
          r := 1;
        If grid[j, k] <= 0 Then
          r := 2;
        field := field+wij[r, c]*grid[j, k]
      End;
    newstate[i] := Htan(field);
  ran := mth$random(seed);

```

```

    If ran <= pac Then
      Begin
        If newstate[i] <= 0 Then
          newstate[i] := conact;
        End;
      End;
    End;
                                { calcampo }

    {----- Main Programa Code -----}
Begin
  seed := clock;
  Write('num,maxx,maxy,maxit: ');
  ReadLn(num, maxx, maxy, maxit);
  Write('g,pac: ');
  ReadLn(g, pac);
  Write('matriz: ');
  ReadLn(wij[1, 1], wij[1, 2], wij[2, 1], wij[2, 2]);
  WriteLn('Working hard...');
  inicia;
  For numit := 1 To maxit Do Begin
    suma := 0;
    suma2 := 0;
    For i := 1 To num Do Begin
      calcampo(i);
      If object[i].e > 0 Then Begin
        suma := suma+1;
        suma2 := suma2+object[i].e;
        es[object[i].x, object[i].y] := es[object[i].x, object[i].y]+1;
      End
    End;
  End;
  For i := 1 To num Do Begin
    object[i].e := newstate[i];
    grid[object[i].x, object[i].y] := newstate[i];
    mueve(i)
  End;
  nact[numit] := suma;
  aai[numit] := suma2
End;
Open(ac);
Rewrite(ac);
For i := 1 To maxit Do
  WriteLn(ac, nact[i]:3:0);
Close(ac);
Open(esp);

```

```
Rewrite(esp);
For i := 1 To maxx Do
  For j := 1 To maxy Do
    WriteLn(esp, es[i, j]:1);
  Close(esp);
End.                                { main program }
```

Appendix B

This Appendix contains the papers on MCA and ants published by this author and that contains additional results.

Miramontes O., Solé R., Goodwin B.C. (1993) “Collective behaviour of random activated mobile celular automata”: *Physica D* **63**: 145-160.

Solé R.V., Miramontes O., Goodwin B.C. (1993), “Oscillations and chaos in ant societies”, *J. Theor. Biol.* **161**: 343-357.

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