

COMPARATIVE ANALYSIS OF THE INTERSPECIFIC AGGRESSIVE  
BEHAVIOUR OF SOME BRITISH ANTS, WITH PARTICULAR  
REFERENCE TO *MYRMICA* SPP. AND *LASTIUS FLAVUS* (F).

A thesis submitted for the degree of  
Doctor of Philosophy.

BY

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"The greatest enemy of ants are other ants, just as the greatest enemy of men are other men..... A strong colony tries to enlarge its domain at its neighbour's expense - to reach their meadows, their trees, etc. This is the source of wars."

Auguste Forel, 1928.

## ABSTRACT

The interspecific aggressive behaviour of some British ants of the genera *Myrmica* and *Lasius* was investigated. Since ants exhibit great variability in their behaviour the main part of the study was concerned with a comparative, numerical analysis of interactions between individuals in controlled laboratory conditions.

Interactions were investigated between individuals and between entire colonies of *M. scabrinodis* and *L. flavus* under various experimental conditions. In this way it was possible to examine a number of factors that were believed to influence aggression such as age, hunger, number of combatants, place of interaction, relative colony size, etc. The experiments have shown how the behaviour of *M. scabrinodis* is adapted to living near to hostile *L. flavus* colonies, and the ecological relationship between the two species in terms of predation and competition in their common, naturally - occurring 'compound' nests is discussed.

The behaviour of individuals of *M. scabrinodis* was examined towards five different ant species that occur in the same habitat. A numerical analysis of the interactions has shown that the intensity of fighting is usually greater in intra- rather than intergeneric encounters. Intraspecific combats are of long duration but, however, lack severity.

The individual behaviour patterns of six closely - related species of the genus *Myrmica* were investigated in interactions with the same opponent species, *L. flavus*. The behavioural relationship of the species to one another was found to be similar to the taxonomic one. However, an exception to this general pattern stressed the need to consider the ecological position of the species in such comparisons.

Finally, the study has shown that several types of responses shown by ants in interspecific interactions must be considered and more than one measurement of these responses may be necessary to gain a true assessment of the aggression present.

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CHAPTER 1

GENERAL INTRODUCTION

## GENERAL INTRODUCTION

"Competition refers to the interaction of 2 organisms striving for the same thing" (Odum, 1953). The ant colony may be regarded as a superorganism (Wheeler, 1911). Ants compete fiercely when either food or nest site is limited. Competition for these resources is reviewed by Brian (1965, page 78). Aggressive behaviour in ants is a widespread and fundamental mechanism employed in both intra and interspecific competition. Much of the competition takes the form of overt fighting. Fighting between different colonies may be fierce, frequent and long-lasting. Many ants will eat other species - half the prey of *Formica subnitens*, for example, consists of other ants (Ayre, 1959). Fighting and mortalities may also result from interference (see Park, 1954) between neighbouring colonies. Many aggressive interactions have been described in the literature (see Forel, 1928, v.2, page 59; Brian, 1965, page 78; Wilson, 1971, page 451) yet surprisingly few observations have involved a quantitative analysis of the behaviour. Holldobler (1976) has examined the length of individual fights between ants in the field. Pontin (1960) has recorded the survival periods of *Lasius niger* and *L. flavus* ~~calate~~ queens in each others' nest. Bhatkar *et al* (1972) established a simple confrontation index between *L. neoniger* and *Solenopsis saevissima* by counting the number of deaths produced from different ratios of combatants. Even fewer studies have considered the actual responses shown by interacting individuals. Wallis (1962a) analysed the aggressive behaviour of *F. fusca* for 4 responses by their frequency of occurrence. De Vroey (1979) has recently carried out a similar study on *Myrmica rubra*.

One of the main aims of this thesis is to undertake a more complete and detailed examination of the interspecific aggressive behaviour of some British ants that commonly occur in the same habitat. This was

attempted by analysing 16 responses shown by ants in interspecific encounters using 3 measurements of behaviour: occurrence, duration and latency. These 3 measurements are frequently used in behavioural studies (Bevan *et al.*, 1960; Hazlett and Bossert, 1965, Dingle, 1969; Gipps, 1977). Additional information was obtained by taking notes, by a temporal analysis, and by counting the number of deaths resulting from behavioural interactions. It was hoped that by such a rigorous analysis that a critical assessment of the measurements of aggression could be made.

Many factors such as hunger (Marikovsky, 1956, 1962b; Wallis, 1962) and temperature (Wallis, 1962), population size, food availability and time of year (De Bruyn, 1968), etc., may influence aggression but because of the lack of detailed studies in carefully controlled conditions they are poorly understood. The study of aggressive behaviour is further complicated by the great variability of individual behaviour within a colony (see Wilson, 1971 page 156). It was, therefore, necessary to carry out comparative studies of interspecific aggressive behaviour in controlled laboratory conditions. Furthermore, because of the variability and complexity of group interactions it was decided that encounters of a comparative nature should be examined between individuals.

The thesis consists of 6 chapters. The first one is this General Introduction. Chapter 2 describes the materials and general method for pair encounters. The following three chapters, 3, 4 and 5, are the experimental ones. Chapter 3 investigates the behavioural relationship between the ants, *M. scabrinodis* and *L. flavus*. These 2 species are frequently found living together in the same nest mound in the wild. In view of the hostility generally found between different ant colonies, which leads to overdispersion when a resource is limited, their behavioural relationship was of particular interest. Behavioural

interactions were first examined between individuals and then between entire colonies of each species. In this way it was hoped to gain a better understanding of how individual behaviour patterns are organised into more complex functional roles in group behaviour. The experiments of this chapter were also designed to investigate some of the more important factors that might influence aggression such as age, hunger, place of interaction, and relative colony size of the interacting species.

Chapter 4 investigates the variability in aggressive behaviour due to the type of opponent encountered. A comparative analysis was made of the behaviour of individual *M. scabrinodis* towards individuals of 4 other species that live in the same habitat. Brian (1965) states that intraspecific competition is more fierce than interspecific competition at a food site and that taxonomically remote species are less likely to meet each other here. The experiments will reflect any inherent, and perhaps learned, differences in behaviour of *M. scabrinodis* towards its different opponents.

The fifth chapter examines the individual behaviour patterns of 6 species of the genus *Myrmica* to a standard stimulus, *L. flavus*. Closely related species are often compared and classified by their morphological characters. Behaviour has no fossil record. By a comparative analysis of the individual behaviour patterns, it is hoped to gain a better understanding of the relationship of species within a genus to one another and perhaps also of the evolution and function of the behaviour.

Discussions appear at the end of each of the 3 experimental chapters. Chapter 6, the General Discussion, relates the 3 chapters to one another and deals with any points left outstanding.

CHAPTER 2

MATERIALS AND GENERAL METHOD

1. Animals Studied.

6 *Myrmica* and 3 *Lasius* species were used in experiments. These were: *M. scabrinodis* Nylander, *M. sabuleti* Meinert, *M. schencki* Emery, *M. rubra* Linnaeus, *M. ruginodis* Nylander, *M. sulcinodis* Nylander, *L. flavus* Fabricius, *L. niger* Linnaeus, and *L. umbratus* Nylander.

Colonies of *M. scabrinodis*, *M. rubra*, *L. flavus* and *L. niger* were obtained from the grounds of the Department of Zoology, Royal Holloway College, Egham, Surrey. The habitat and distribution of ants in this area has been described by Pontin (1969). An additional nest of *M. scabrinodis* was taken from chalk grassland at Chalton Hill, Hampshire.

The ant *M. ruginodis* was taken from the 'Great Wood', Callow Hill, Virginia Water, Surrey.

Nests of *M. sulcinodis* came from the heath at Arne, Dorset.

Colonies of *M. sabuleti* were found in chalky grassland areas of the Chilterns near Christmas Common, Oxfordshire.

Three nests of *M. schencki* were obtained from Femmøller, Zyland, Denmark. The ant was abundant in this area and inhabited a light soil, often among colonies of *L. flavus*.

A colony of *L. umbratus* was acquired from the heath at Chobham Common, Surrey.

A fuller account of the habitat and distribution of these ants is given by Donisthorpe (1927), and a distribution atlas is compiled by Barrett (1977).



2. Laboratory housing of the animals.

Colonies of the above species comprising workers, <sup>physogastric</sup> queen and brood, were excavated and transferred to artificial nests where they could be observed and manipulated more easily. A variety of artificial nests has been designed (Brian, 1977; Chauvin, 1972; Pontin, 1962; Skaife, 1961). The type chosen for use in this study is illustrated below in Figure 1. The nest area was made of either plaster of paris or cement, depending on the moisture requirements of the species. A plastic sandwich box was used as a foraging area and this was connected to the nest by a transparent plastic tube. A band of polytetrafluoroethylene (Fluon) was smeared around the sides of the foraging area to prevent the ants escaping. Food was always readily available to the ants. This consisted of a 5 - 10% soln. of sugar and honey. Concentrations higher than this could have caused the ants to 'dry up' afterwards (Brian, 1977). A small amount of D. melezytose dihydrate powder was added to the carbohydrate solutions to improve taste and acceptability (Pontin, 1978). Protein was supplied to the ants in the form of adult *Drosophila melanogaster* and pupae of *Tenebrio* sp. A 'complete synthetic diet' for ants is given by Ettershank (1967). Feeding habits have been reviewed by Stradling (1978). The stock nests were housed in a basement room where experiments were later performed.

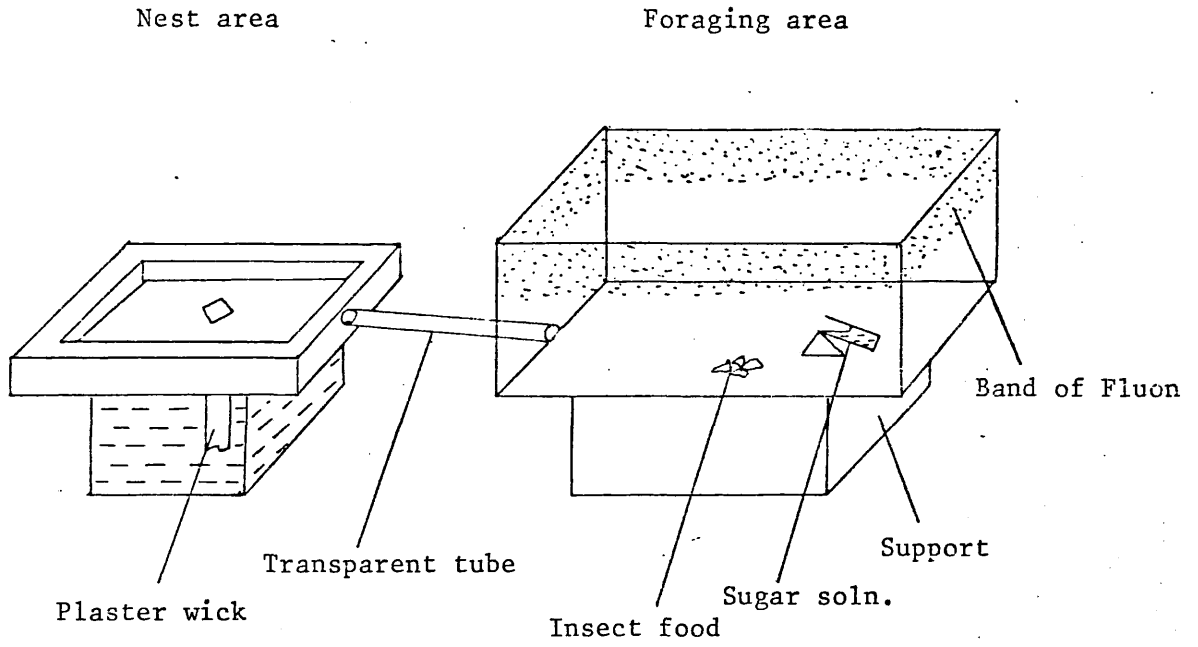


FIGURE 1. Artificial ant nest

3. General method for pair encounters.

3.1. Apparatus.

(i) The experimental arena.

The place of interaction between ants was considered to be a very important factor influencing aggression. All experiments of a comparative nature were, therefore, carried out in a standard situation. Experimental arenas were made for this purpose (plate 1). Two arenas, each measuring 5 x 2 x 0.5cms, were machined, side by side, out of a perspex block. The arenas were connected to each other at one end but could be separated by a sliding partition. The roof of the arena consisted of a small sheet of glass.

(ii) The recording apparatus.

A ten channel ink pen event recorder<sup>\*</sup> was chosen to record the behavioural responses of animals in interspecific encounters. This type of recorder was relatively much cheaper than ones with more recording channels. It was possible by 'pairing' some channels and varying signals to record the 17 responses that were required.

A keyboard with 10 switches was made to transfer visual observations of behaviour manually onto the permanent record of the recorder's paper chart. 7 keys were 'lever type' microswitches<sup>\*\*</sup> and had plastic discs glued on the ends of the levers. 3 keys were 'push-button illuminated latching switches' which were useful in monitoring responses of long duration (e.g. locomotion.). 3 relays were needed in conjunction with the latching switches as the latter had a low current carrying capacity.

A mains driven power pack was made to supply the 12 volts direct current that was required by the event recorder and relays.

The keyboard, powerpack, event recorder and paper chart are shown in plate 2 .

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\* (Aero Services Ltd, Type H30)

\*\* (R.S. Components Ltd)

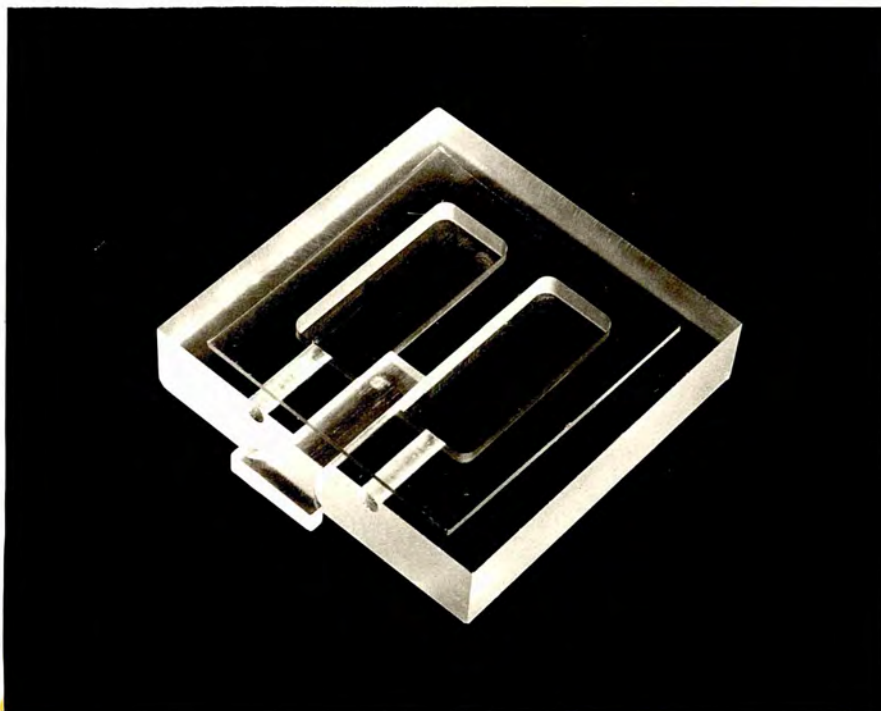


PLATE 1. The experimental arena.

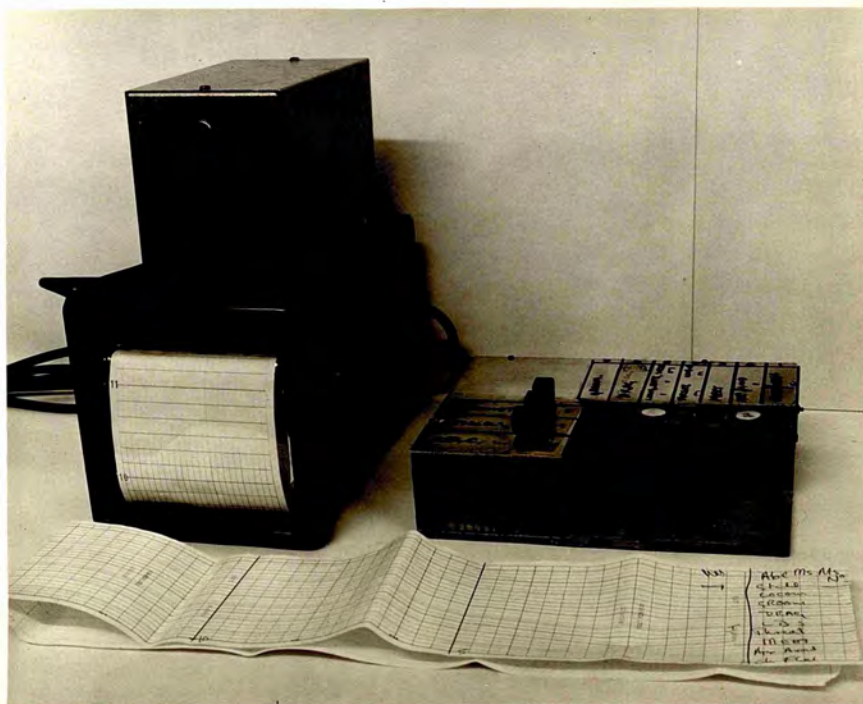


PLATE 2. The recording apparatus.

The recorder was run at a speed of 3 cm per minute. A sequence of occurrences could then be distinguished when separated by only  $\frac{1}{2}$  a second and the chart was kept to a convenient length.

### 3.2. Procedure

Interactions between 2 species of ant were examined in the experimental arena. One ant of each species was selected (see 3.1.9) ) by presenting it with a soft artist's paint brush onto which it climbed and transferred from the foraging area to a separate arena of the apparatus. In this way the possible risk of injury was minimised. The animals were introduced into the arena from above and a piece of glass was slid over to prevent them escaping. Although great care was taken when moving the animals, because ants are sensitive to even the slightest disturbance, a settling down period was thought to be necessary before each experimental encounter. The time required by the ants to settle down in this particular apparatus was found by examining their rate of activity in the open field (see 3.1.1. ). A 15 minute period was considered suitable for this purpose. The partition separating the 2 arenas was carefully removed after the adjustment period so that the ants could meet one another, by chance, during exploratory activity. The partition was closed when the ants met and the ensuing behaviour between the unfamiliar pair was observed within 1 arena for a 30 minute period. The behaviour of one species was recorded in detail using the event recorder. When a response was seen to occur the relevant switch on the keyboard was depressed and sustained for the duration of the response. The responses recorded on the paper chart were later examined by hand and 3 measurements of behaviour were taken. Notes on the behaviour of both species were taken where appropriate. Ten replicate trials were done for each experiment. Species A was introduced into the arena occupied by species B in 5 trials and vice versa in the other 5 trials. Any difference due to this factor was investigated. Both

ants were placed in a small glass tube (5 x 1cm), containing a piece of damp tissue paper to prevent desiccation after the encounter and left there for 24 hours. Their health was noted at the end of this period.

### 3.3. Variables controlled.

The following conditions were observed in addition to the place of interaction, food state and settling down time mentioned above:

- 1) The temperature in the experimental room was maintained at  $20^{\circ}\text{C} \pm 1^{\circ}\text{C}$  by a fan heater\*. Brian (1977) suggests this to be an ideal temperature for *Myrmica* culture. The ants were soon thought to habituate to the continual noise produced by the heater.
- 2) No windows were present in the experimental room. Lighting was kept constant. The light was governed by a time switch,\*\* and a 60-watt bulb shone from 6am to 9pm daily. Rhythms in ants are discussed by Grabensberger (1933), Ayre (1958), Harker (1961) and Sudd (1967).
- 3). Pieces of thick sponge were placed inbetween parts of experimental apparatus to reduce land-borne sounds to which ants are particularly sensitive.
- 4) Encounters were between unfamiliar pairs and so each ant was only used in one experiment.
- 5) Only animals that seemed to be in good health were selected.
- 6) Experiments were performed between 10am and 4pm.
- 7) The arena and paint brushes were thoroughly washed in hot water and detergent, rinsed and dried after each experiment.
- 8) *Myrmica* species are relatively monomorphic while *Lasius* show a greater degree of polymorphism. Only individuals of each species of comparable size and headwidth were chosen.

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\* Sunvic controls Ltd., Type F102-3.

\*\* Verner Auto Point serial No. HH9440.

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9) It is well known that workers of a nest may differ greatly on their behaviour. The ants were placed into discrete ethal groups based on 3 criteria :

- a) Age - *Myrmica* workers were aged according to the degree of cuticle pigmentation. This method was also used to give a rough idea of the age of the *Lasius* species. This technique has been used in *Myrmica* by Weir (1958) and Tricot (1974a). The different melanic groups recognised in *M. scabrinodis* and *L. flavus* are shown in plates 3 and 4.
- b) Location - Ants were chosen according to where they were found in the colony. That is: 1) in the foraging area, 2) inside the nest and away from the brood, 3) inside the nest and near to the brood. Location of an ant has been shown to be related to aggression by Dobrzanska, (1959). Age may also be related to location (Otto, 1958).
- c) Aggression - Ants were chosen depending on whether or not they attacked the artist's brush presented to them.

The pair encounter experiments investigated the behaviour of the older, most deeply pigmented ants that were found in the foraging area and that attacked the artist's brush.

Some experiments investigated the behaviour of younger *Myrmica* and *Lasius* taken from inside the nest, which did not usually attack the paint brush. A special note is made where this occurs.

#### 3.4. Categories of Behaviour.

Prior observations of interactions between ants indicated that the behaviour could be classified into several distinct responses (acts). A description of the acts is given below. A note was made when a particular species performed a given act in a slightly different manner



PLATE 3 Pigmentary (ethal) groups of *Myrmica scabrinodis*.



PLATE 4. Pigmentary (ethal) groups of *Lasius flavus*.



to that described.

- 1) MEET. An encounter involving recognition\* and either contact or close proximity of the individuals to one another.
- 2) APPROACH. Encounters were often a result of chance meetings during locomotory activity. APPROACH is the recognition and deliberate movement by one species towards the other.
- 3) AVOIDANCE. This is the recognition and deliberate movement by one species away from the other. The action is often jerky and may involve a sharp withdrawal of the antennae or body.
- 4) THREAT. The ant's head is raised, its jaws are open and the posture is directed towards the opponent. The antennae are usually held forward but their actual position and state of activity is variable. The legs are often spread and the body has an elevated posture.
- 5) LUNGE. This behaviour involves a short rapid forward movement of the body and the ant attempts but does not succeed in biting its opponent. The action may be feeble and the jaws only partly open before the strike.
- 6) BITE. An attack in which the ant's mandibles hold the opponent for a duration no greater than one second.
- 7) SEIZE. An attack in which the ant's mandibles hold the opponent for any duration greater than one second.
- 8) DRAG. This behaviour is exhibited when SEIZE is combined with a locomotory element. Intended dragging, where the opponent resists the active pulling of the aggressor, is also included in this category.
- 9) STING. This behaviour occurs with either the SEIZE or DRAG response. The abdomen is curled beneath the body inbetween the legs and its tip is pressed against the opponent. Whether or not the sting is actually everted or contents emitted is not recorded.

---

\* Recognition usually occurs when the ants are within 5cms of one another. It is judged to take place when an ant stops and shows direct orientation of the antennae towards the opponent.

- 10) CHASE. The rapid pursuit of one individual by another immediately after a meeting is termed CHASE. The antennae are active and the jaws are held open in this response.
- 11) FLEE. This is the rapid locomotion by an individual after a meeting away from its opponent. The antennae are active and the jaws are closed.
- 12) GROOM. Any self-cleaning movements performed by the animal are scored as GROOM.
- 13) LOCOMOTION. Any walking movements performed by the animal other than DRAG, CHASE and FLEE.
- 14) ABDOMEN-CURLING IN LOCOMOTION. The abdomen is flexed beneath the body during fast locomotory activity. The response is shown by only 2 species to any extent.
- 15) STILL. The ant ceases its activity and remains motionless for a period of time. The behaviour is usually shown in the presence of an opponent. Various forms of the STILL response are shown by the ants but in all cases the jaws are closed. All forms are recorded as the STILL response and a description of each is given in the relevant sections.
- 16) ABDOMEN-CURLING. The abdomen is curled beneath the body and the ant remains motionless with jaws closed.  
Both the STILL and ABDOMEN-CURLING responses are sometimes referred to as the 'passive responses'.
- 17) CONFLICT. This response is scored when either the STILL or ABDOMEN-CURLING acts are shown but with the jaws open. The word 'CONFLICT' is a description of the ant's posture and no attempt is made at this stage to interpret the motivation or intention of the animal.

Acts written in capital letters in this thesis refers to the actual definitions given above, otherwise the general meaning of the word is intended.

### 3.5. Measurements of the behavioural responses.

The following 3 measurements were used to record the responses shown

by the test animal in experimental pair encounters :

- 1) Latency. The time interval (in seconds) from the beginning of the encounter to when the behavioural response first occurred.
- 2) Occurrence. The total number of times that a behaviour occurred in the encounter.
- 3) Duration. The total amount of time (in seconds) spent performing the behaviour in the encounter.

### 3.6. Statistical analysis.

The encounters were of finite length and sometimes responses were not shown by animals in some replicate trials. The zero scores were meaningful and had to be included in the analysis. Thus the results were frequently not normally distributed. Transformations were investigated without success. Non-parametric statistics were, therefore, necessary.

#### (i) Temporal patterning.

The temporal patterning of each of the 16 responses shown by test animals in the 30 minute experimental period was examined for both occurrence and duration using the Friedman 2-way Analysis of variance test.\* The encounters were divided into 6 x 5 minute periods, and the scores shown in each period for the 10 replicate trials were compared with each other. A 10 x 6 matrix was therefore analysed.

#### (ii) Comparison of 'pair encounters'

The responses shown in 2 types of experimental encounter were compared with each other using the Mann-Whitney U test.\* The scores from the 10 replicate trials of each encounter were compared for each response and for each of the 3 measurements of behaviour.

\* Siegel, 1956.

(iii) The CONFLICT response.

a) The amount of time that an ant spent performing CONFLICT behaviour in the MEET and INTER-MEET periods was examined by the Wilcoxon paired rank test\*. The scores from the MEET and INTER-MEET periods were first expressed as a percentage of the total duration of the respective periods. The Wilcoxon test was then used to rank the values of only the replicate trials that showed the CONFLICT behaviour. A trial where the ant did not perform CONFLICT was excluded from the analysis.

b) The CONFLICT response was sustained after a meeting by some animals. The termination or further sustainment of the response on the arrival of the opponent was analysed by the Binomial test\*. Animals from replicate trials that did not sustain the behaviour in the INTER-MEET period were excluded from the analysis.

Other statistical tests used infrequently are given in the relevant sections. Statistical tests employing the Friedman 2-Way Analysis of Variance and the Mann-Whitney U test were carried out using a computer because of the large amount of data involved. Programs for each test were written and all raw data was transferred onto punched cards for the analysis.

\*see Siegel, 1956.

CHAPTER 3

BEHAVIOURAL INTERACTIONS BETWEEN *M. SCABRINODIS* AND *L. FLAVUS*.

1. Introduction.

A brief account follows on the ecology and habits of *M. scabrinodis* and *L. flavus* which is thought necessary before considering the relationship between them.

*L. flavus*, the 'yellow hill' or 'turf' ant is typically found in dry, sunny situations (Donisthorpe, 1927; O'Rourke, 1950; Gaspar, 1971). The nests are often large and may contain 10,000 (Odum and Pontin, 1961), 24,000 (Waloff and Blackith, 1962) or even 100,000 (Nielsen, 1976) workers. Colonies may occur in very high densities — distribution studies have been done by Waloff and Blackith (1962), Gallé (1972) and Elmes (1974). The ant is a very proficient builder and constructs large nest mounds, elaborate in structure, to gain a higher nest temperature for brood development. The ant may also nest beneath stones (Wilson, 1955). The mound is the centre of a feeding territory (Carey and Diver, 1937; Pickles, 1937) which is considered by Pontin (1961) to be essentially 2 dimensional. *L. flavus* is a completely subterranean species and feeds on a variety of root aphids in this territory by taking their honeydew and by preying on them (Pontin, 1953). The ants, therefore, rarely venture above ground.

*M. scabrinodis*, like *L. flavus*, prefers to nest in dry, warm, sandy places (Wasmann, 1891; Donisthorpe, 1927; O'Rourke, 1950; Gaspar, 1971) although the species shows a wide range of tolerance (Elmes, 1975). The colonies are much smaller in size than those of *L. flavus*. Elmes finds nests of 200 - 300 workers to be the most common but emphasises that great variation exists. Pickles (1936) has recorded nests of 200 - 2,000 workers. The distribution of this ant has been described by Donisthorpe (1927). *M. scabrinodis* may build small nest mounds to a height of around 5cms. (Brian, 1958) but the ant is usually found in exposed

places, on heaths and banks, beneath stones and in the nests of other ants. Although the ant feeds to an extent on underground aphids, much of its foraging is done above ground where it feeds on both aphids and insect prey (Pickles, 1936).

*M. scabrinodis* has for a long time been known to inhabit the same nest mound as *L. flavus*. (Gould, 1747; Smith, 1855; Freyer, 1913; Donisthorpe, 1927; Pontin, 1969). The 2 species are often found nesting together beneath the same stone (Farren-White, 1883; Donisthorpe, 1902). The *Myrmica* can, and often does, live independently. Most authors agree that the red ant lives in a distinct part of the *L. flavus* nest and that their quarters are quite separate. Donisthorpe (1902) reports that if the stone is removed from their nest, thus exposing the ants to each other, the 2 species will fight. Further indication of hostility between the 2 species is present in the literature. Forel (1928) and Donisthorpe (1913) have recorded the build-up of large numbers of *L. flavus* head capsules on the refuse pile of the red ant. O'Rourke (1950) states that *M. scabrinodis* will rob *L. flavus* nests and kill the workers for food. Pontin (1969) removed *M. scabrinodis* nests from *L. flavus* mounds and found a significant increase in alate queen production of *L. flavus* there the following year. There is, therefore, strong evidence to suggest that *M. scabrinodis* is preying on *L. flavus*, but the relationship between the species may be a more complex one. A comprehensive review of the different relationships of ants in both 'compound' and 'mixed' nests is given by Wilson (1971).

The following experiments in this chapter were performed to investigate the relationship between *M. scabrinodis* and *L. flavus*, to study the individual and group behaviour patterns of the ants and to examine some of the factors which might influence aggression.

2. Experimental Section.

2.1. Exploratory behaviour.

2.1.1. Introduction.

Much importance has been placed on exploration in studies of vertebrate behaviour (Nissen, 1954; Thorpe, 1963; Harlow, 1954; Butler, 1960).

Locomotion has been much used as a measurement of exploratory behaviour in both vertebrates (Montgomery, 1953 and 1954; Berlyne, 1955 and 1960) and insects (Darchen, 1952 and 1955). Gross locomotory activity without reference to spatial characters is commonly used in the 'open field' (Thompson, 1953). Three experiments were done to examine the exploratory activity of *M. scabrinodis* and *L. flavus*.

In the first 2 experiments, the rate of locomotion is employed to investigate the exploratory behaviour of *M. scabrinodis* and *L. flavus*. The experiments are carried out in an 'open field' situation. This is the experimental arena in which interspecific aggressive encounters were later performed. The experiments were performed for 3 reasons:

- a) To investigate and compare the activity rates of individuals of the 2 species in the open field.
- b) To compare the activity rates of solitary ants with that of ants in pair encounters.
- c) To determine the length of time that the animals would need to adjust to the new environment (arena).

The ants could then be given this 'settling-down' time in pair encounter experiments before being introduced to each other (see 'General Method', page 7 ).

The third experiment investigates, both qualitatively and quantitatively, the various responses shown by solitary *M. scabrinodis* and *L. flavus* during exploration of the arena for both old and young workers and also analyses the grooming behaviour of *M. scabrinodis* in detail.



2.1.2. Locomotory rate of solitary workers

(i) Method.

The locomotory rate of solitary workers of *M. scabrinodis* and *L. flavus* was investigated in the experimental arena. An ant of oldest age group was taken from its foraging area and placed in the arena. The glass roof of the arena had been marked into 5mm lattice squares. The number of squares that the animal entered per minute were recorded for a 30 minute period. The ants were sometimes stationary (e.g. still or grooming). Only the actual locomotory rate was considered. Thus:

$$\text{Activity rate} = \text{No. of squares entered} \times \frac{60}{\text{Time (secs. per min.) spent performing locomotion}}$$

The locomotory rate was examined for 10 individuals of each species.

(ii) Results.

The mean activity rates of solitary *M. scabrinodis* and *L. flavus* in the open field (arena) are displayed in Figure 2. Both species performed locomotion persistently throughout the 30 minute period. The graph shows that the activity rate of each species was high initially and that this decreased with time. There appears to be little change in the rate of activity in both species after around 15 minutes. A 15 minute period was, therefore, judged to be adequate for the ants to settle down in the arena before experimental encounters (see 'General Method', page 7 ).

The activity rates of the 2 species were found to be significantly different from one another\* ( $p < 0.001$ ,  $t = 3.89$ ,  $df = 58$  ). The speed of *L. flavus* was almost twice that of *M. scabrinodis* throughout the experimental period.

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\* Students t-test.

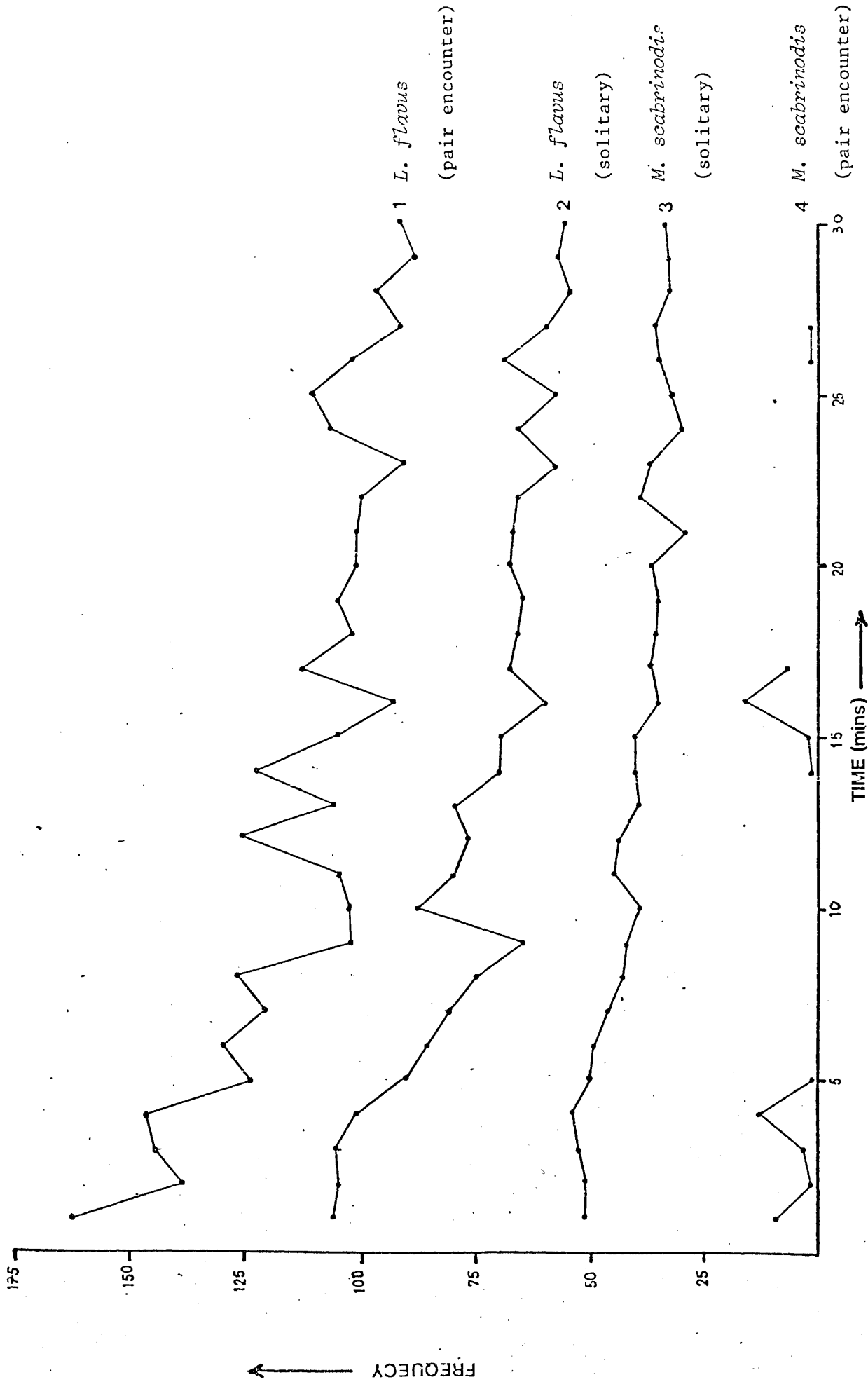


FIGURE 2 Mean locomotory rate of *M. scabrinodis* and *L. flavus* individuals when alone, and when in pair encounters with each other (n = 10).

2.1.3. Locomotory rate of ants in pair encounters.

(i) Method.

The locomotory activity of *M. scabrinodis* and *L. flavus* was examined in pair encounter situations. An ant of each species was placed in a separate arena and, after a 15 minute adjustment period, the species were introduced to one-another (see 'General Method', page 7 ). The locomotory rate of each ant was recorded simultaneously using the open field technique described above. Ten replicate trials were performed.

(ii) Results

The mean activity rates of *M. scabrinodis* and *L. flavus*, when present together in a pair encounter situation, are shown in Figure 2. The results show that an encounter between individuals of these 2 species has a dramatic effect on their exploratory (locomotory) activity.

*L. flavus* becomes much more excited and runs at a much faster rate when the opponent is present. This activity rate is very high initially and seems to decrease with time. Furthermore, this activity is still much higher after 30 minutes than it is in experiments where no opponent is present.

The activity of *M. scabrinodis* is, in contrast, greatly reduced by the presence in the arena of *L. flavus*. The ant is often motionless for long periods. When *M. scabrinodis* did perform locomotion it was often done in a slow, seemingly hesitant, manner. The activity rates of the 2 *Lasius* groups when compared\* are statistically very different from each other ( $p < 0.05$ ,  $t = 2.14$ ,  $df = 58$  ).

---

\* Students t-test

Table 1. The relative frequency and duration of 3 responses performed by solitary ants of 4 experimental groups during exploration.

Type of ant	% Occurrence			% Duration		
	LOCOMOTION	GROOM	STILL	LOCOMOTION	GROOM	STILL
<i>M. scabrinodis</i> (old)	50.6	46.6	2.8	89.0	4.0	7.0
<i>M. scabrinodis</i> (young)	45.4	43.2	11.4	60.8	7.7	31.5
<i>L. flavus</i> (old)	68.8	31.2	0.0	93.4	6.6	0.0
<i>L. flavus</i> (young)	45.5	47.1	7.0	37.2	47.5	15.3

2.1.4. Behavioural responses shown during exploration.

(i) Method.

The responses shown by solitary workers of *M. scabrinodis* and *L. flavus* during exploratory behaviour in the arena were investigated. Both old and young animals of each species were examined. A single animal was placed in the arena and its behaviour was recorded with the above exceptions, as in the 'General Method.' Ten replicate trials were done for each of the 4 experimental groups. The 4 experimental groups were then compared with one another. The grooming behaviour of old and young *M. scabrinodis* was also examined (see below 2.1.5.).

The responses shown by solitary ants in the arena were later considered when analysing the responses shown by ants in pair encounters.

(ii) Results.

The 4 experimental groups of animals performed only 3 responses to any extent during exploratory activity. These responses were LOCOMOTION, STILL and GROOM. The relative number of occasions and amount of time that each ant group spent showing each of the 3 responses are given in Table 1.

The 3 responses are shown as a percentage of their combined totals for each of the 2 measurements and for each experimental group of animals.

The experimental groups are statistically compared with respect to these responses in Tables 2 - 7.

a) The effect of age on exploratory behaviour.

Differences in exploratory behaviour due to age were found in both *M. scabrinodis* and *L. flavus* (Tables 2 and 3, respectively.) Older workers of both species show locomotion for longer, and spend less time grooming themselves than do younger workers.

In addition, younger *L. flavus* remain motionless more often and for longer than older ones do.

b) Exploratory behaviour of the 2 species.

The exploratory behaviour of *M. scabrinodis* and *L. flavus* is compared for old and young age groups in Tables 4 and 5, respectively.

Older animals of each species seemed to explore the arena in a similar way to one another; no significant differences can be found in the persistent LOCOMOTION and little amount of STILL behaviour that each performed. Although both species performed short bouts of grooming activity at intervals, *L. flavus* did so for longer periods each time ( $p < 0.01$ ).

Young animals of the 2 species also behaved in a similar way to each other during exploratory activity.. No differences can be found in their LOCOMOTION and STILL responses but, as with older animals, young *L. flavus* GROOM themselves for far longer periods than do young *M. scabrinodis*.

c) Age and species effect.

Tables 6 and 7 compare the exploratory behaviour of older workers of one species with that of younger workers of the other species. It

Tables 2 - 7. Comparison of the responses shown during exploratory activity by solitary ants of 2 experimental groups. The tables show the Mann-Whitney Statistic (U), the associated probability (P) and the group (G) having the higher score. (n = 10) (see page 26 for key).

Table 2. *M. scabrinodis* (old) vs. *M. scabrinodis* (young)

Response	OCCURRENCE			DURATION		
	U	P	G	U	P	G
GROOM	25	NS	-	20.5	*	2
LOCOMOTION	27	*	1	14	**	1
STILL	33	NS	-	32	NS	-

Table 3. *L. flavus* (old) vs. *L. flavus* (young)

Response	OCCURRENCE			DURATION		
	U	P	G	U	P	G
GROOM	40	NS	-	85	***	2
LOCOMOTION	38	NS	-	0	***	1
STILL	20	*	2	20	*	2

Table 4. *M. scabrinodis* (old) vs. *L. flavus* (old)

Response	OCCURRENCE			DURATION		
	U	P	G	U	P	G
GROOM	46	NS	-	18.5	**	2
LOCOMOTION	46	NS	-	30.5	NS	-
STILL	40	NS	-	40	NS	-

Table 5. *M. scabrinodis* (young) vs. *L. flavus* (young)

Response	OCCURRENCE			DURATION		
	U	P	G	U	P	G
GROOM	32	NS	-	8	***	2
LOCOMOTION	32	NS	-	28	NS	-
STILL	45.5	NS	-	41	NS	-

Table 6. *M. scabrinodis* (old) vs. *L. flavus* (young)

Response	OCCURRENCE			DURATION		
	U	P	G	U	P	G
GROOM	44.5	NS	-	4	***	2
LOCOMOTION	40	NS	-	9	***	1
STILL	35.5	NS	-	35.5	NS	-

Table 7. *L. flavus* (old) vs. *M. scabrinodis* (young)

Response	OCCURRENCE			DURATION		
	U	P	G	U	P	G
GROOM	22	*	2	45	NS	2
LOCOMOTION	22	*	1	13	**	1
STILL	20	*	2	20	*	2

Key to all tables employing the Mann-Whitney U test.

\*  $p < 0.05$

\*\*  $p < 0.02$

\*\*\*  $p < 0.002$

N.S. not significant

n.a. not applicable.

The null hypothesis ( $H_0$ ) is that the samples A and B from 2 populations have the same distribution. The alternative hypothesis is a directional hypothesis ( $H_1$ ) that one sample is stochastically larger than the other. The test is considered to be two-tailed for one cannot assume beforehand which sample will have the greater value. i.e. it is desirable to know whether  $A > B$  or  $B > A$ .

can be seen that in both cases older workers of one species perform LOCOMOTION for longer durations and GROOM for less time than younger workers of the other species. Also, older *L. flavus* are motionless less often and for less time than are young *M. scabrinodis*.

2.1.5. Grooming activity of *M. scabrinodis*.

(i) Method.

The grooming activity of *M. scabrinodis* was examined during exploratory behaviour experiments. Observations were carried out on both old and young animals. Grooming activities were classified for analysis in the following way:

- a) Individual Antennal Cleaning (I.A.C.); Either the right or the left antenna is cleaned, one or more times, through the ipsilateral fore tarsus and spur.
- b) Dual Antennal Cleaning (D.A.C.); Both antennae are cleaned, as above, in the same sequence. Occasionally, both antennae are groomed simultaneously.
- c) Fore tarsal Cleaning (F.T.C.); The fore tarsi are drawn through the lower mouthparts.
- d) Fore tarsi and antennal cleaning (F.T.A.C.); Grooming of the antennae and fore tarsi in the same sequence.
- e) Other Cleaning Acts. (O.C.A.); Any self-grooming activity other than the above 4 categories; these include cleaning of the body and abdomen.

The number of times that each grooming act was performed by the ant in the 30 minute period was recorded. The frequencies of the acts were then compared with one another using the Friedman 2-Way Analysis of Variance. Antennal cleaning was further investigated by recording the number of times that each antenna was drawn through the tarsal spur per grooming sequence. The frequency distribution was again analysed by the Friedman 2-Way Analysis of Variance.



(ii) Results.

The frequencies of the different grooming responses shown by old and young *M. scabrinodis* in exploratory activity are given in Table 8. It can be seen that both age groups groom some parts of the body significantly more often than others.

Table 8. Frequency of the grooming acts shown by old and young *M. scabrinodis* during exploratory behaviour.

Grooming acts.	<i>M. scabrinodis</i> (old) <i>M. scabrinodis</i> (young)	
Individual antennal cleaning (left)	47	9
Individual antennal cleaning (right)	67	22
Dual antennal cleaning	21	9
Foretarsal cleaning	18	33
Foretarsal and antennal cleaning	8	12
Other cleaning acts	-	35
	83%	33%
	17%	67%
Friedman Statistic ( $\chi^2$ )	11.5	14
Significance Level	p<0.05	p<0.02

Table 9. Frequency of antennal cleaning movements per single bout of activity shown by *M. scabrinodis* during exploratory activity.

	<i>M. scabrinodis</i> (old) <i>M. scabrinodis</i> (young)	
One Stroke	22	21
Two Strokes	119	76
Three Strokes	33	22
Four Strokes	13	2
$\chi^2$	14.4	20
Significance level	p<0.01	p<0.001

Older animals, as stated above, performed short bouts of grooming inbetween otherwise persistent locomotion. Table 8 shows that this grooming is mainly of the antennae (83%). Furthermore, usually only one antenna is cleaned in a bout of activity. Dual antennal cleaning and foretarsal cleaning are done to a lesser extent. 'Other cleaning acts', such as grooming of the abdomen, thorax or legs are rarely, if ever, seen.

The grooming activity of younger ants was quite different from that of older ants. Younger ants groomed for relatively longer periods of time and the grooming usually comprised a wider variety of cleaning responses. The 'fore-tarsal cleaning' and 'other cleaning acts' were performed significantly more than other cleaning responses. Indeed, the abdomen and legs were often groomed by younger animals.

Antennal cleaning is further examined for both age groups in Table 9. It is clear that both age groups, when cleaning the antennae, have a strong preference for passing them through the tarsal spurs twice.

## 2.2. Interactions between individuals.

### 2.2.1. Interactions between foragers.

#### (i) Introduction and Method.

As older workers are generally believed to be the most aggressive members of a colony so interactions were first examined between the oldest age groups of each species. Individuals of *M. scabrinodis* and *L. flavus* were taken from their respective foraging areas and placed in the experimental arenas. Encounters between them were observed following the procedure of the 'General Method'. The responses shown by *M. scabrinodis* were recorded in detail and notes on both species were taken, where appropriate.

#### (ii) Results.

The behaviour of ants in this experiment was similar in all replicate trials. A typical encounter is therefore, described:

The ants met, apparently by chance, during locomotory activity. *L. flavus* always approached and made a contact examination of the *Myrmica* with rapid antennal activity. Attempts were made to investigate all parts of the *Myrmica* and this often involved climbing on and over its body. The *Lasius* threatened, bit, seized and attempted to drag its opponent a great deal. The abdomen was not curled beneath the body and therefore acid was not directly used in attacks. Aggressive acts were of short duration and of low intensity and attacks were not considered to be fierce. *L. flavus* showed a willingness to fight at each meeting throughout the 30 minute encounter.

Mean scores for the responses shown by *M. scabrinodis* in pair encounters with *L. flavus* are given in Table 10.

*M. scabrinodis*, in contrast, showed very little aggression towards the *Lasius*, with the result that fighting between the ants did not take

TABLE 10. Mean Scores for the responses shown by individuals of *M. scabrinodis* in pair encounters with *L. flavus*, (n = 10)

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	4.2	n.a.
AVOID	2.9	n.a.
MEET	27.0	743.4
THREAT	0.8	7.0
CONFLICT	4.1	114.8
LUNGE	0.0	n.a.
BITE	0.0	n.a.
SEIZE	0.0	0.0
DRAG	0.0	0.0
STING	0.0	0.0
CHASE	0.0	n.a.
FLEE	0.0	n.a.
GROOM	2.5	24.4
LOCOMOTION	4.0	209.0
STILL	4.5	176.6
ABDOMEN CURLING	12.4	1340.0

place. Indeed, the acts LUNGE, BITE, SEIZE, DRAG, STING and CHASE were never shown. *M. scabrinodis* became motionless on being examined, and adopted either the STILL or ABDOMEN CURLING posture (see Plates 5 and 6). These relatively 'passive' acts were performed and sustained at each meeting. The duration of meetings was therefore determined by *L. flavus*. The *Myrmica* often sustained its 'passive' postures after the opponent had departed for very long periods (see Figures 4 and 5, pages 63 and 64.). When locomotion was performed after a meeting it was done in a 'normal' unhurried manner and with slow deliberate antennal movements. The ants showed no signs of injury after interactions, for example by sporadic or excited activity, and all animals were alive and seemingly uninjured after 24 hours.

APPROACH and AVOID were both shown by *M. scabrinodis*, usually when the *Lasius* was either unaware of its presence or not directing aggression towards it. The *Myrmica* sometimes attempted to turn slowly towards the opponent while performing a 'passive' response. Further stimulation from the *Lasius* stopped this attempted orientation. THREAT was sometimes shown at the beginning of a meeting before actual contact took place. When *L. flavus* approached and attacked, the threatening behaviour of the *Myrmica* ceased. CONFLICT was not shown in the initial minutes of the encounter but thereafter much was performed. The CONFLICT response (see plate 7) was shown in both the presence and absence of the *Lasius* (see Figure 6), page 65 ). Furthermore, when CONFLICT was sustained in the INTER-MEET period it was often terminated when the opponent next approached (see Figure 7 page 66 ). The *Myrmica* behaved in a passive way in meetings throughout the encounter. No significant changes in the temporal patterning of any responses could be found (see Appendix, Table 2).

The 3 responses, GROOM, LOCOMOTION and STILL, performed by *M. scabrinodis* in 'exploratory behaviour' were shown to a very different



PLATE 5. STILL response shown by *M. scabrinodis* on being attacked by  
*L. flavus*.

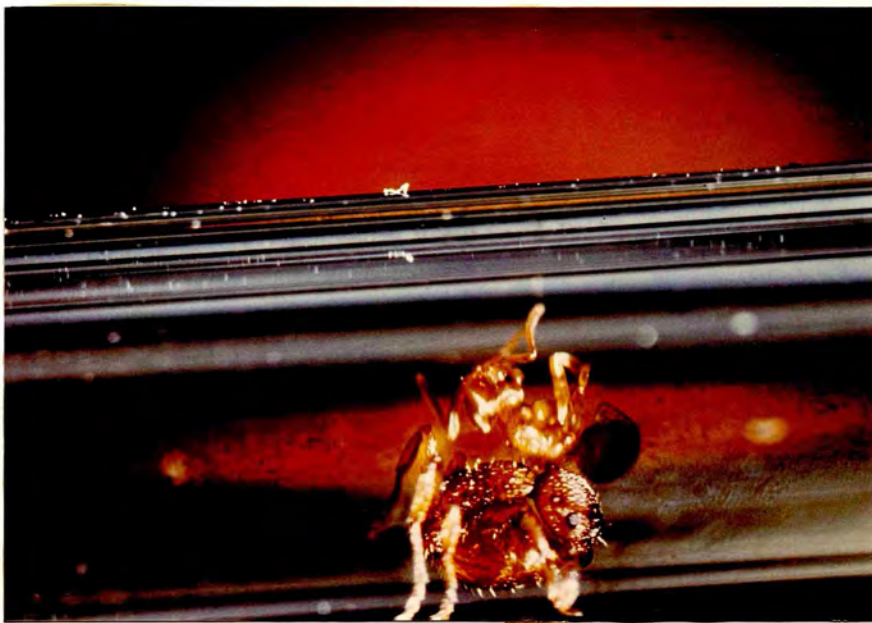


PLATE 6. ABDOMEN-CURLING response shown by *M. scabrinodis* on being attacked  
by *L. flavus*.



PLATE 7. CONFLICT response shown by *M. scabrinodis* on being attacked by *L. flavus*.

workers are also the first to leave a disturbed nest. They have a higher locomotory rate and are more likely to approach and examine a strange object than are younger ones.

extent when an opponent was present in the arena (see Table 11). The ant moved around much less, groomed less and was still for much longer when *L. flavus* was present.

TABLE 11. Comparison of the 3 responses shown by individuals of *M. scabrinodis* in exploratory behaviour, and in the presence of *L. flavus* in pair encounters (see page 26 for key).

Behavioural Response	Occurrence			Duration		
	U	P	G	U	P	G
GROOM	0.0	***	1	14.5	**	1
LOCOMOTION	14.0	**	1	1.0	***	1
STILL	21.0	***	2	22.0	*	2

2.2.2. The influence of age on interactions between individuals.

(i) Introduction and Method.

Individuals of a colony may differ from each other in their behaviour (polyethism) and exhibit job preferences (Sudd, 1967; Wilson, 1971; Carrol, 1973). The variation in behaviour affecting division of labour is seen by Wilson (1971) to consist of 3 components - polymorphism, age polyethism and all remaining variation. A mass of literature exists both on polymorphism (see Kennedy, 1961, and Schmidt, 1974) particularly with reference to aggression (Creighton, 1959; Dobrzanska, 1959; Vowles, 1955; Wilson, 1962 and 1968; Weber, 1972), and on age polyethism (Buckingham, 1911; Erdhart, 1931; Ledoux, 1949; Otto, 1958; Wier, 1958; Dobrzanska, 1959; Jander, 1967; Tricot, 1974). Age has been strongly correlated with the degree of aggressiveness in ants. Weir (1958) with *Myrmica ruginodis*, Dobrzanska (1959) with *Formica sanguinea* and Tricot (1975) with *M. rubra* have all found that older workers are the most aggressive members of a colony. These old workers are also the first to leave a disturbed nest, they have a higher locomotory rate and are more likely to approach and examine a strange object than are younger ones.



The following 2 experiments were performed to investigate the effect of age on interactions between *M. scabrinodis* and *L. flavus*. The first experiment records, in detail, the behaviour of old *M. scabrinodis* towards young *L. flavus* and the second that of young *M. scabrinodis* towards old *L. flavus*. The 2 ethal/age groups of ants were selected using the criteria described on page 11 . The pair encounter experiments were carried out following the 'General Method'.

(ii) Results.

a) *M. scabrinodis* (old) vs. *L. flavus* (young).

Mean scores for the responses shown by *M. scabrinodis* in encounters with young *L. flavus* are given in Table 12 . The ants behaved in a similar way throughout the period and no significant difference in temporal patterning of any act could be found (see Appendix, Table 4). It can be seen that the behaviour of *M. scabrinodis* was very similar towards both old and young *Lasius*. Exactly the same responses were performed with each. The ant became passive in meetings and sustained the posture after the opponent had departed (see Figs 4 and 5, pages 63 and 64). No fighting occurred and all ants were alive and seemingly healthy after 24 hours. The CONFLICT response was shown in a different way to each age group. An older *Lasius* usually inhibited the response in meetings while a younger one did not. Thus CONFLICT was shown most during INTER-MEET periods with the former but often during the MEET periods with the latter (see Figure 6 1) and 3), page 65 ). The responses shown by *M. scabrinodis* in encounters with old and young *L. flavus* are quantitatively compared in Table 13 . Significant differences are present. ABDOMEN-CURLING is shown sooner, more often, and for longer when with an older opponent and STILL behaviour correspondingly less. More CONFLICT was performed with a younger opponent and meetings were also of longer duration here.

The behaviour of a young *L. flavus* worker was observed to be quite

TABLE 12 Mean Scores for the responses shown by individuals of *M. scabrinodis* in pair encounters with young *L. flavus*, (n = 10).

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	4.2	n.a.
AVOID	1.4	n.a.
MEET	25.9	1074.2
THREAT	0.8	14.8
CONFLICT	2.1	185.6
LUNGE	0.0	n.a.
BITE	0.0	n.a.
SEIZE	0.0	0.0
DRAG	0.0	0.0
STING	0.0	0.0
CHASE	0.0	n.a.
FLEE	0.0	n.a.
GROOM	2.3	37.0
LOCOMOTION	12.4	301.8
STILL	12.9	496.4
ABDOMEN CURLING	7.2	728.2

TABLE 13. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH *M. scabrinodis* vs. *L. flavus*  
 (test animal) (opponent) (test animal) (opponent) (young)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	33.0	N.S.	-	44.0	N.S.	-	n.a.	-	-
AVOID	46.0	N.S.	-	36.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	33.5	N.S.	-	17.0	**	2
THREAT	42.0	N.S.	-	43.0	N.S.	-	43.0	N.S.	-
CONFLICT	28.0	N.S.	-	26.5	N.S.	-	31.0	N.S.	-
LUNGE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
BITE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
SEIZE	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
DRAG	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
STING	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
CHASE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
FLEE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
GROOM	47.0	N.S.	-	46.5	N.S.	-	47.0	N.S.	-
LOCOMOTION	39.0	N.S.	-	37.5	N.S.	-	38.5	N.S.	-
STILL	15.5	**	2	12.5	**	2	25.0	N.S.	-
ABDOMEN CURLING	24.0	N.S.	-	23.5	N.S.	-	16.0	**	1

different to that of its older sister in encounters with *M. scabrinodis*. On meeting, it did not immediately approach and attack the opponent, which was typical of the older group, but instead became motionless and threatened some 3 millimeters away. The head was raised, the jaws were wide open and the antennae were held forward. The *Lasius* usually sustained the threatening response for very long periods. Its legs were sometimes raised and lowered in a 'flicking' action for no apparent reason. When the *Myrmica* approached, very slowly, the *Lasius* either withdrew to the same distance away as before or attacked. Attacks by the *Lasius* were not considered to be fierce.

b) *M. scabrinodis* (young) vs. *L. flavus* (old).

Mean scores for the responses shown by the young *M. scabrinodis* are given in Table 14. The ant was considered to behave in a similar way throughout the encounter and no significant differences could be found in the temporal patterning of the acts (see Appendix, Table 3). It can be seen that the behaviour of old and young *M. scabrinodis* towards *L. flavus* was basically the same. Both age groups performed exactly the same responses in encounters. Passive behaviour was shown, fighting did not take place, and the animals were always alive and well after 24 hours. The sustainment of the passive acts are shown for comparison in Figures 4 and 5 (pages 63 and 64.). The responses of old and young *M. scabrinodis* towards *L. flavus* are quantitatively compared in Table 15. The similarity in the behaviour of the 2 age groups is further reflected in this analysis where few significant differences are found. However, differences are present in 2 important responses. CONFLICT is shown more often and for longer by older animals. ABDOMEN-CURLING is also shown for longer periods and the STILL response less often and for less time.

The behaviour of *L. flavus* was considered to be similar to both

TABLE 14. Mean Scores for the responses shown by young individuals of *M. scabrinodis* in pair encounters with *L. flavus*. (n = 10),

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	3.5	n.a.
AVOID	0.8	n.a.
MEET	23.9	698.2
THREAT	0.6	2.8
CONFLICT	1.0	8.0
LUNGE	0.0	n.a.
BITE	0.0	n.a.
SEIZE	0.0	0.0
DRAG	0.0	0.0
STING	0.0	0.0
CHASE	0.0	n.a.
FLEE	0.4	n.a.
GROOM	1.4	13.6
LOCOMOTION	12.4	335.4
STILL	13.7	562.4
ABDOMEN CURLING	9.2	835.8

TABLE 15. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH *M. scabrinodis* (young) vs. *L. flavus*  
 (test animal) (opponent) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	38.0	N.S.	-	38.5	N.S.	-	n.a.	-	-
AVOID	45.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	31.5	N.S.	-	43.0	N.S.	-
THREAT	35.0	N.S.	-	41.5	N.S.	-	40.0	N.S.	-
CONFLICT	28.5	N.S.	-	22.0	*	1	22.0	*	1
LUNGE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
BITE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
SEIZE	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
DRAG	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
STING	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
CHASE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
FLEE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
GROOM	39.0	N.S.	-	39.0	N.S.	-	45.0	N.S.	-
LOCOMOTION	38.5	N.S.	-	37.5	N.S.	-	34.5	N.S.	-
STILL	29.0	N.S.	-	9.0	***	2	15.0	**	2
ABDOMEN CURLING	28.5	N.S.	-	33.5	N.S.	-	16.0	**	1

old and young *M. scabrinodis*. Each type of opponent was readily attacked.

### 2.2.3. The influence of hunger on interactions between individuals.

#### (i) Introduction and Method.

Hunger, a physiological need and indicator of body state, sets up an internal stimulus in the animal - the primary feeding drive. By starving animals the motivation level is increased. With an increase in deprivation the response threshold is lowered so that weak stimuli that do not normally initiate a response may then do so. Lorenz (1973) states that hunger lowers the threshold for killing. Hunger can influence the behaviour of ants at both the individual and colony level. Starved workers of *Formica fusca* show an increase in cleaning, movement and other responses and also a greater readiness to forage (Wallis, 1962b). A hungry ant on discovering food becomes intensely active and on returning to the nest boosts the activity of the colony. Wheeler (1910) states hunger as one of the main stimuli to increased activity. *F. polycetena* workers increase in number near the nest exits at a time of food shortage (Otto, 1958) and Butler and Free (1952) have recorded the same occurring in bees

The following experiment investigates the effect of hunger on the aggression/predation shown by *M. scabrinodis* towards *L. flavus* in pair encounters. The laboratory colony of *M. scabrinodis* was deprived of food, but allowed water, for 2 weeks before experiments were undertaken. The colony of *L. flavus* was well fed during this period. The behaviour of hungry workers of *M. scabrinodis* was recorded in pair encounters with *L. flavus*.

#### (ii) Results.

Mean scores for the responses shown by hungry *M. scabrinodis* in encounters with *L. flavus* are given in Table 16. The ant was thought to react in a similar way towards the opponent throughout the period.

TABLE 16. Mean Scores for the responses shown by hungry individuals of *M. scabrinodis* in pair encounters with *L. flavus*.  
(n = 10).

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	6.2	n.a.
AVOID	0.2	n.a.
MEET	27.8	818.0
THREAT	3.2	6.4
CONFLICT	0.1	1.2
LUNGE	0.2	n.a.
BITE	0.2	n.a.
SEIZE	0.4	1.5
DRAG	0.0	0.0
STING	0.0	0.0
CHASE	0.0	n.a.
FLEE	0.0	n.a.
GROOM	1.3	24.4
LOCOMOTION	14.5	358.0
STILL	17.2	434.2
ABDOMEN CURLING	12.9	960.0



TABLE 17. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH *M. scabrinodis* (Hungry) vs. *L. flavus*  
 (test animal) (opponent) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	44.0	N.S.	-	47.0	N.S.	-	n.a.	-	-
AVOID	34.0	N.S.	-	22.5	*	1	n.a.	-	-
MEET	n.a.	-	-	48.5	N.S.	-	49.0	N.S.	-
THREAT	35.0	N.S.	-	45.0	N.S.	-	41.5	N.S.	-
CONFLICT	29.0	N.S.	-	17.0	**	1	16.5	**	1
LUNGE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
BITE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
SEIZE	30.0	N.S.	-	30.0	N.S.	-	30.0	N.S.	-
DRAG	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
STING	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
CHASE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
FLEE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
GROOM	34.0	N.S.	-	36.5	N.S.	-	40.0	N.S.	-
LOCOMOTION	38.0	N.S.	-	29.5	N.S.	-	28.0	N.S.	-
STILL	41.0	N.S.	-	6.0	***	2	20.0	*	2
ABDOMEN CURLING	34.0	N.S.	-	48.5	N.S.	-	17.0	**	1

No significant differences can be found in the temporal patterning of each response (see Appendix, Table 5 ).

Hungry ants behaved in a similar way to satiated ones. The passive responses were performed in meetings and sustained after the opponent had departed (see Figures 4 and 5, pages 63 and 64). All ants were alive and seemingly healthy after 24 hours. However, some differences in behaviour were apparent. Very little THREAT and CONFLICT was seen in hungry animals. Also, a small proportion of the ants did LUNGE, BITE and SEIZE the *Lasius* although fighting was generally rare. No interactions were fierce and locomotion, when present, was done in a slow and deliberate manner.

The responses of hungry and satiated animals are quantitatively compared in Table 17 . Hungry animals AVOID less, and the CONFLICT response is shown less often and for less time than by a satiated ant. ABDOMEN-CURLING is performed for less time and the STILL response correspondingly more often and for longer by the hungry group. No significant differences other than these can be found.

The behaviour of *L. flavus* was believed to be the same towards hungry and satiated opponents. The *Lasius* approached and attacked the opponent at each meeting.

#### 2.2.4. The influence of numbers on individual interactions.

##### (i) Introduction and Method.

Ants when in groups often modify the physiology and behaviour of each other (Chen, 1937; Grassé *et al* 1944; Hess 1942) The aggressiveness of social insects has been shown to increase as the number of nest mates grows. Solitary workers of *Acanthomyops claviger* are almost insensitive to alarm substances but respond normally if many other workers are present (Wilson, 1971). Small colonies or groups of *Crematogaster lineolata* are timid and take refuge when disturbed but become very fierce in larger groups (Wheeler, 1906).

In the previous pair encounter experiments individuals of *M. scabrinodis* did not usually attack *L. flavus* and, indeed, showed very little aggression towards them. The following experiment examines the behaviour of a group of 9 *M. scabrinodis* workers towards a single *L. flavus* in the experimental arena.

Nine *M. scabrinodis* workers were selected and placed in a glass tube (7.5 x 2.5cms). After a few minutes they were transferred to one of the experimental arenas. A single *L. flavus* worker was taken and placed in the second arena. After a 'settling down' period the partition was removed so that the ensuing interactions occurred within both areas. The behaviour of all ants was filmed by video tape recording for 30 minutes. Afterwards, the tape was re-run 9 times and on each occasion the behaviour of a separate *M. scabrinodis* worker was documented by the event-recording apparatus.

Because of problems with the depth of field and resolution at high magnification imposed by the video apparatus, and because it was sometimes necessary to observe 'postures' from different angles, it was not possible to measure accurately THREAT and CONFLICT behaviour. Direct observational notes were taken instead. Consequently, statistical analysis of THREAT and CONFLICT was not made.

With the exception of the above details the General Method was closely followed.

Five replicate trials of the experiment were performed to gain more details of the behaviour and 'fate' of *L. flavus* but with no further analysis of the *Myrmica* behaviour.

The behaviour of *M. scabrinodis* in this experiment was compared with its behaviour in a pair encounter situation (i) with *L. flavus* (experiment 2.2.1 and (ii) when starved with satiated *L. flavus* (experiment 2.2.

ii) Results.

Mean scores for the responses shown by the nine *M. scabrinodis* in encounters with one *L. flavus* are displayed in Table 18 . Analysis of the temporal patterning of these responses is given in Appendix, Table 6. Responses that changed significantly with time (see Figure 3 ) are described below.

The *Myrmica* usually performed either the STILL or ABDOMEN-CURLING response on meeting the opponent, as they did in pair encounters.

Both the STILL and ABDOMEN-CURLING responses were often sustained after the opponent had departed (see Figures 4 and 5 , respectively). Locomotion was performed, inbetween bouts of 'passive' behaviour, in an unhurried manner and with slow antennal movements. The ants spent almost all of their time performing these 3 responses. All 3 responses showed a temporal patterning. The temporal effect seen in these 3 acts may be related to the number and durations of meetings. Meeting occurred far more in the initial minutes of the encounter - the length of meetings was determined by *L. flavus*.

Various types of communication were seen to take place between the *Myrmica* workers. Antennal contact occurred when the ants were both moving around and stationary in groups. Stationary ants occasionally tapped their abdomens repeatedly and quickly on the floor of the arena. The abdomen was also seen pressed to the ground and the lance extruded during some bouts of locomotion.

The attraction of workers towards the *Lasius* was marked. The AVOID and FLEE responses were never shown. The animals approached significantly more in the initial minutes of the encounter; however, meetings were also more frequent at that time. Several *Myrmica* often

TABLE 18. Mean Scores for the responses shown by individuals of *M. scabrinodis* in encounters with *L. flavus* (9:1 ratio of combattants).

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	7.2	n.a.
AVOID	0.0	n.a.
MEET	19.0	28.9
THREAT	0.0	0.0
CONFLICT	0.0	0.0
LUNGE	0.0	n.a.
BITE	0.2	n.a.
SEIZE	0.3	6.6
DRAG	0.0	0.0
STING	0.0	0.0
CHASE	0.0	n.a.
FLEE	0.0	n.a.
GROOM	1.2	11.8
LOCOMOTION	1.4	36.0
STILL	15.7	418.6
ABDOMEN CURLING	11.1	778.8

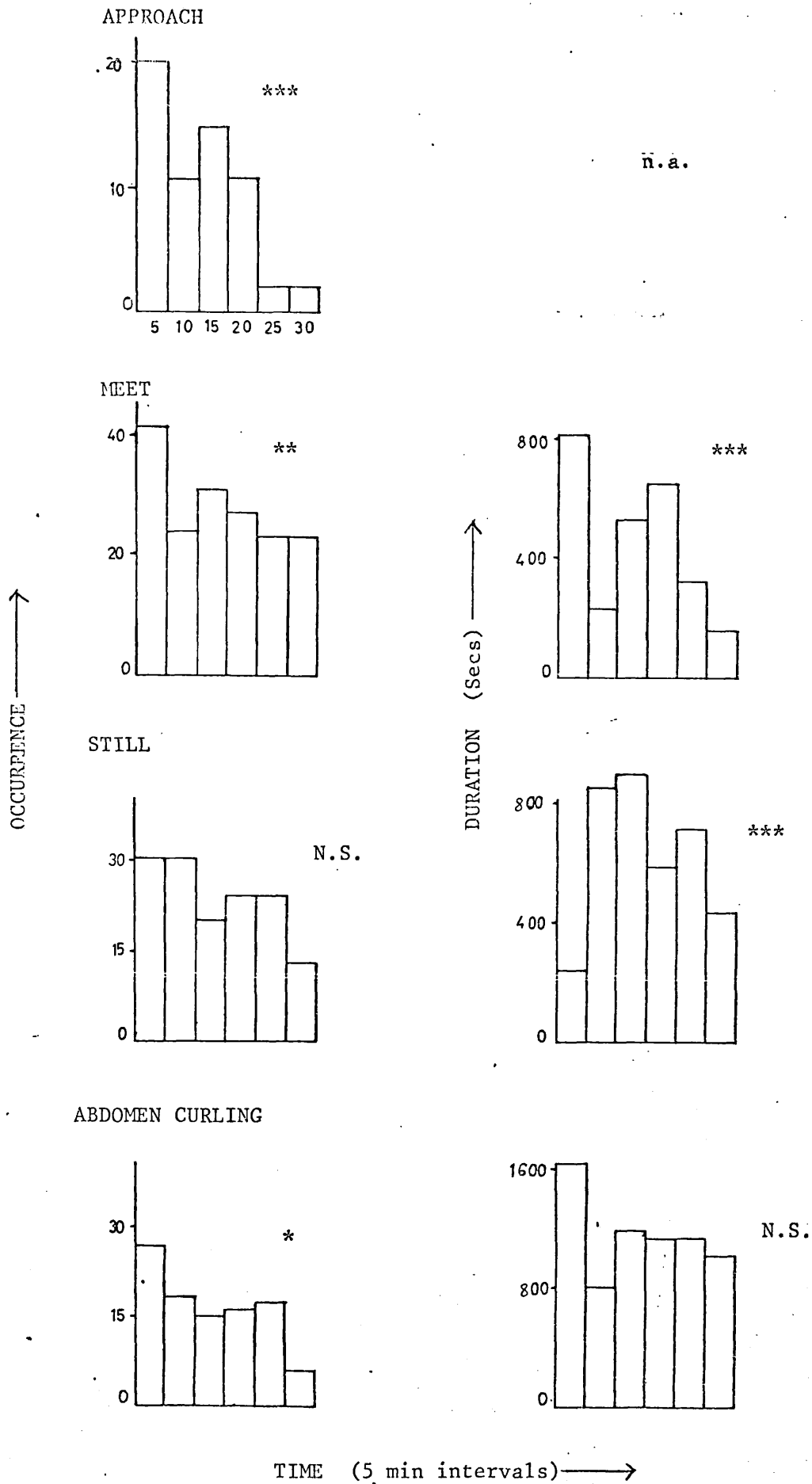


FIGURE 3. Temporal patterning of responses shown by *M. scabrinodis* in 30 minute encounters with *L. flavus*. (9:1 ratio of combatants.

(see Key page 50).

Key to all figures and tables employing the Friedman 2-Way Analysis  
of Variance test for the analysis of temporal patterning of behavioural  
responses.

\*  $p < 0.05$

\*\*  $p < 0.01$

\*\*\*  $p < 0.001$

N.S. Not significant

n.a. Not applicable

The null hypothesis is that there is no observable difference in the ants behaviour with time. That is, the scores shown in the 6 x 5 minute periods of a 30 minute experimental encounter are drawn from the same population. The associated probability is determined by reference to the chi-square distribution.

approached the *Lasius* from different directions. The movement was slow and often could only be detected by the increasingly stretched position of the legs. The *Myrmica* stopped approaching and showing THREAT when the *Lasius* attacked them. The *Lasius* could not 'subdue' all ants simultaneously, with the result that it often became closely surrounded. (see plate 8 ). On many occasions the heads of the *Myrmica* were almost touching the body of the *Lasius*. The jaws were sometimes partly open and antennae held forward in this position; otherwise, the ants remained relatively passive. Although the *Myrmica* approached and showed this grouping behaviour a great deal the *Lasius* was rarely attacked. The responses SEIZE and CHASE were exhibited on only 3 occasions and LUNGE, BITE, DRAG and STING were never seen. All ants were alive and well after each experimental encounter. However, 2 of the 5 *Lasius* were found dead after 24 hours.

The behaviour of *L. flavus* was similar in all trials. Initially, the ant was extremely active and showed rapid locomotion. This high activity was considered to decrease with time. The *Lasius* avoided the opponents at first but soon after readily approached and attacked them as it did a solitary opponent in pair encounters. The ant then continued to be aggressive throughout the encounter. The ant bit, seized and pulled at the *Myrmica* a great deal but rarely used its gaster in attacks. The high level of aggression was shown even when several opponents were closely grouped around it. The ant displayed 'freedom of movement' in such group interactions by climbing over and walking away from the opponents at will.

Comparison of the behaviour of individuals within a group with that of solitary ones.

The behaviour of solitary *M. scabrinodis* towards *L. flavus* would seem to be different in some ways from its behaviour when a number of its sisters are present. A quantitative analysis of the individual



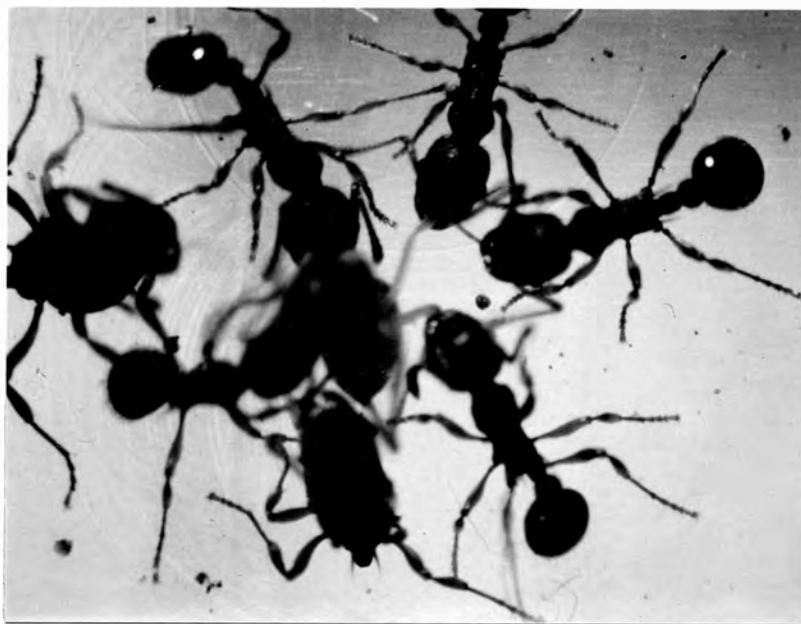


PLATE 8. Grouping behaviour of *M. scabrinodis* around a solitary  
*L. flavus*.

TABLE 19 Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH *M. scabrinodis* vs. *L. flavus*  
 (test animal) (opponent) (test animal) (opponent) (9:1 Ratio)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	24.0	N.S.	-	41.5	N.S.	-	n.a.	-	-
AVOID	37.0	N.S.	-	22.5	*	1	n.a.	-	-
MEET	n.a.	-	-	14.0	**	1	5.0	***	1
THREAT	n.a.	-	-	n.a.	-	-	n.a.	-	-
CONFLICT	n.a.	-	-	n.a.	-	-	n.a.	-	-
LUNGE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
BITE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
SEIZE	35.0	N.S.	-	35.0	N.S.	-	35.0	N.S.	-
DRAG	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
STING	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
CHASE	35.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
FLEE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
GROOM	48.5	N.S.	-	33.0	N.S.	-	40.5	N.S.	-
LOCOMOTION	30.0	N.S.	-	26.5	N.S.	-	18.0	**	2
STILL	35.0	N.S.	-	7.5	***	2	18.0	**	2
ABDOMEN CURLING	49.0	N.S.	-	40.0	N.S.	-	8.0	***	1

TABLE 20 Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* (Hungry) (test animal) (opponent) COMPARED WITH *M. scabrinodis* vs. *L. flavus* (9:1 Ratio) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	22.0	*	2	31.5	N.S.	-	n.a.	-	-
AVOID	49.5	N.S.	-	40.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	5.0	***	1	7.0	***	1
THREAT	n.a.	-	-	n.a.	-	-	n.a.	-	-
CONFLICT	n.a.	-	-	n.a.	-	-	n.a.	-	-
LUNGE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
BITE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
SEIZE	45.0	N.S.	-	45.0	N.S.	-	45.0	N.S.	-
DRAG	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
STING	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
CHASE	35.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
FLEE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
GROOM	40.0	N.S.	-	40.0	N.S.	-	49.0	N.S.	-
LOCOMOTION	35.0	N.S.	-	39.0	N.S.	-	42.0	N.S.	-
STILL	34.0	N.S.	-	34.5	N.S.	-	39.0	N.S.	-
ABDOMEN CURLING	27.0	N.S.	-	44.0	N.S.	-	30.0	N.S.	-

versus group behaviour is given in Table 19 . It can be seen that several differences are present. A 'group' animal approaches an enemy sooner and avoids it less often than does a solitary ant. Locomotion is also performed more frequently and for longer periods with respect to the former. Group members show ABDOMEN-CURLING for less time but the STILL response more often and for longer than do solitary individuals. Meetings between opponents in the 'group' experiment occur less often and for less time than they do in pair encounters. This is understandable as the *Lasius* has to distribute its time between 9 opponents rather than just 1. In fact, overall meetings occur 6 times more often and for 3 times longer in 'group' experiments than in pair encounters.

Comparison of the behaviour of individuals within a group with that of solitary hungry ones.

The behaviour of hungry, solitary animals towards an opponent was similar to that of individuals in a group. The ants became passive in the majority of interactions, in both cases. In both experimental groups the ants often approached and rarely avoided the *Lasius*. Furthermore, ants of both groups bit and seized the opponent to a very small extent. The responses of the 2 experimental groups are compared numerically for 3 measurements in Table 20 . Meetings occur more often and for longer between animals of the 'group' experiment, and these animals also approach the enemy sooner than a hungry solitary ant does. No other differences in responses other than these were found.

2.2.5. The behaviour of *M. scabrinodis* towards corpses of 2 *Lasius* species.

(i) Introduction and Method.

Ants are extremely diverse in their feeding habits (see Stradling, 1978). While some species are indiscriminate feeders and take both live and dead prey, others such as *Tapinoma sessile*, *Solenopsis molesta* and

*Myrmica americana* have a definite preference for dead or dying animals.

The literature reports *M. scabrinodis* carrying *L. flavus* corpses but actual aggression towards or predation on the ant is not noted.

The previous experiments have revealed that individuals and small groups of *M. scabrinodis* show very little aggression towards a single aggressive *L. flavus* in a neutral area. The following 2 experiments investigate the behaviour of individual *M. scabrinodis* towards corpses of *L. flavus* and *L. niger* to determine (i) the extent to which aggression is influenced by the activity of the opponent (ii) whether or not the ant behaves differently to 2 very differently 'smelling' opponents of the same genus.

The behaviour of *M. scabrinodis* towards dead workers of (i) *L. flavus* and (ii) *L. niger* was investigated following the 'General Method' for pair encounters. Preliminary observations indicated that encounters of 15 minutes were adequate to show the behaviour occurring. The *Lasius* were killed by crushing the thorax with a blunt scalpel, taking care not to rupture the body excessively. The bodies were left for 20 minutes before being placed in the arena. The ant would, undoubtedly, release pheromones when being killed. Morgan *et al* (1978) states that the head of a decapitated ant will 'continue to live' and emit pheromones for 15 minutes. Other substances released from a possible wound were not considered.

(ii) Results.

a) Behaviour towards corpses of *L. flavus*.

Mean scores of the responses shown by *M. scabrinodis* in encounters of 15 minutes with dead *L. flavus* are given in Table 21. None of the responses showed a temporal patterning (Appendix, Table 7).

The *Myrmica* approached and examined, or avoided and ignored the dead ant at various times. Fleeing behaviour did not occur. The corpse was

TABLE 21. Mean scores for the responses shown by *M. scabrinodis* to live and dead *L. flavus* in 15 minute pair encounters (n = 10).

RESPONSE	OCCURRENCE		DURATION	
	LIVE	DEAD	LIVE	DEAD
APPROACH	1.4	0.9	n.a.	n.a.
AVOID	1.6	3.0	n.a.	n.a.
MEET	13.8	8.5	420.4	312.0
THREAT	0.3	1.7	3.4	7.6
CONFLICT	1.7	1.6	25.2	87.2
LUNGE	0.0	1.0	n.a.	n.a.
BITE	0.0	0.4	n.a.	n.a.
SEIZE	0.0	4.0	0.0	97.8
DRAG	0.0	1.2	0.0	39.8
STING	0.0	0.8	0.0	15.2
CHASE	0.0	n.a.	0.0	n.a.
FLEE	0.0	0.0	0.0	n.a.
GROOM	0.9	4.8	16.0	80.2
LOCOMOTION	5.2	8.7	99.4	382.2
STILL	3.8	3.2	105.0	102.6
ABDOMEN CURLING	6.3	0.6	665.4	29.2

sometimes inspected for a brief period after which the *Myrmica* proceeded to explore the arena. The ant spent the vast majority of its time performing locomotion in a 'normal' unhurried manner. Many of the ants displayed aggression towards the corpses. Only a small amount of THREAT was performed and this was usually seen for a brief period in initial meetings. On subsequent meetings the corpse was examined with closed jaws. CONFLICT was sometimes shown in interactions and sustained for long periods. Very little CONFLICT was shown by the *Myrmica* away from the corpse.

A proportion of the ants seized and carried the corpse. Stinging actions were observed but the lance was not thought to have been extruded. Moreover, the stinging movement was rather slow and sustained, resembling the ABDOMEN-CURLING posture rather than the quick flexing action typical of stinging. Much grooming accompanied aggressive bouts. Many parts of the body were cleaned and the bouts often lasted for some time. The ant performed the STILL and ABDOMEN-CURLING responses very little during meetings and rarely during the INTER-MEET periods.

b) Behaviour to live and dead *Lasius flavus*.

Mean scores for the responses shown by *M. scabrinodis* to live and dead *L. flavus* in 15-minute encounter periods are shown in Table 21 . The responses are statistically compared in Table 22 .

The ant's behaviour was very different towards live and dead *L. flavus*. The *Myrmica* usually performed a 'passive' response on meeting a live opponent and sustained the act for long periods. ABDOMEN-CURLING was done very much less and later on when with a dead opponent. The live *L. flavus* was believed to restrict the activity of *M. scabrinodis* and to govern the length of meetings between them. Meetings occurred less often and both grooming and locomotion were shown more and sooner

TABLE 22. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH *M. scabrinodis* vs. *L. flavus* (Dead)  
 (test animal) (opponent) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	47.0	N.S.	-	15.5	**	2	n.a.	-	-
AVOID	10.0	***	2	26.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	20.0	*	1	26.0	N.S.	-
THREAT	38.0	N.S.	-	28.0	N.S.	-	35.0	N.S.	-
CONFLICT	49.5	N.S.	-	46.5	N.S.	-	50.0	N.S.	-
LUNGE	25.0	N.S.	-	25.5	N.S.	-	n.a.	-	-
BITE	30.0	N.S.	-	25.5	N.S.	-	n.a.	-	-
SEIZE	35.0	N.S.	-	35.0	N.S.	-	35.0	N.S.	-
DRAG	40.0	N.S.	-	40.0	N.S.	-	40.0	N.S.	-
STING	40.0	N.S.	-	40.0	N.S.	-	40.0	N.S.	-
CHASE	n.a.	-	-	n.a.	-	-	n.a.	-	-
FLEE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
GROOM	17.0	**	2	13.5	**	2	22.0	*	2
LOCOMOTION	6.5	***	2	26.5	N.S.	-	17.5	**	2
STILL	39.5	N.S.	-	48.5	N.S.	-	37.0	N.S.	-
ABDOMEN CURLING	8.0	***	1	1.0	***	1	0.0	***	1
L.B.S.D.St	15.0	**	2	15.0	**	2	15.0	**	2



with a dead ant. Furthermore, a corpse was approached much more and avoided sooner than was a live animal. The combined aggressive responses (L, B, S, D, St, Ch ) were shown significantly more towards dead than towards live opponents. Live *Lasius* were never attacked while dead ones were both attacked and carried around.

c) Behaviour towards corpses of *L. niger*.

Mean scores for the responses shown by *M. scabrinodis* in 'encounters' with dead *L. niger* are given in Table 23. None of the responses show a temporal patterning (Appendix, Table 8 ).

*M. scabrinodis* behaved in several different ways on meeting the corpse. The *L. niger* was often avoided or ignored and the ant continued walking in a normal unhurried manner. Fleeing was not observed. Sometimes the corpse was approached cautiously and THREAT was shown for a brief period. All ants examined the corpses at some stage but only a proportion seized and carried them. Interactions with corpses did not involve excited or erratic activity. Stinging behaviour was done by only 1 ant. Grooming was performed and for a short duration each time. The ABDOMEN-CURLING response never occurred and the STILL response was seen on only a few occasions. CONFLICT behaviour was also not recorded. Further analysis of the CONFLICT and 'passive' responses was not necessary. The *Myrmica* spent most of its time performing locomotion.

d) Comparison of the behaviour of *M. scabrinodis* towards corpses of the 2 *Lasius* species.

The responses shown by *M. scabrinodis* towards corpses of *L. flavus* and *L. niger* are compared in Table 24 . No significant differences in any of the responses can be found. The ant was believed to behave in a similar way to each of the species with the possible exception of the CONFLICT and STILL acts. The Table shows that these 2 acts have

TABLE 23. Mean Scores for the responses shown by individuals of *M. scabrinodis* in pair encounters with dead *L. niger* (n = 10).

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	0.6	n.a.
AVOID	6.3	n.a.
MEET	8.5	231.8
THREAT	1.7	8.0
CONFLICT	0.0	0.0
LUNGE	0.0	n.a.
BITE	0.9	n.a.
SEIZE	3.9	73.4
DRAG	2.2	133.6
STING	2.4	23.0
CHASE	n.a.	n.a.
FLEE	0.0	n.a.
GROOM	6.3	17.4
LOCOMOTION	13.4	599.2
STILL	1.2	13.6
ABDOMEN CURLING	0.0	0.0

TABLE 24. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. niger* (Dead) COMPARED WITH *M. scabrinodis* vs. *L. flavus* (Dead)  
 (test animal) (opponent) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	38.0	N.S.	-	36.0	N.S.	-	n.a.	-	-
AVOID	46.0	N.S.	-	33.5	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	44.0	N.S.	-	41.0	N.S.	-
THREAT	42.5	N.S.	-	40.0	N.S.	-	37.5	N.S.	-
CONFLICT	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
LUNGE	40.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
BITE	42.5	N.S.	-	46.5	N.S.	-	n.a.	-	-
SEIZE	45.5	N.S.	-	49.5	N.S.	-	47.5	N.S.	-
DRAG	42.5	N.S.	-	46.0	N.S.	-	44.0	N.S.	-
STING	42.5	N.S.	-	46.0	N.S.	-	46.0	N.S.	-
CHASE	n.a.	-	-	n.a.	-	-	n.a.	-	-
FLEE	45.5	N.S.	-	50.0	N.S.	-	n.a.	-	-
GROOM	36.5	N.S.	-	49.5	N.S.	-	44.0	N.S.	-
LOCOMOTION	49.5	N.S.	-	32.5	N.S.	-	33.5	N.S.	-
STILL	32.5	N.S.	-	28.5	N.S.	-	29.0	N.S.	-
ABDOMEN CURLING	45.5	N.S.	-	40.0	N.S.	-	40.0	N.S.	-

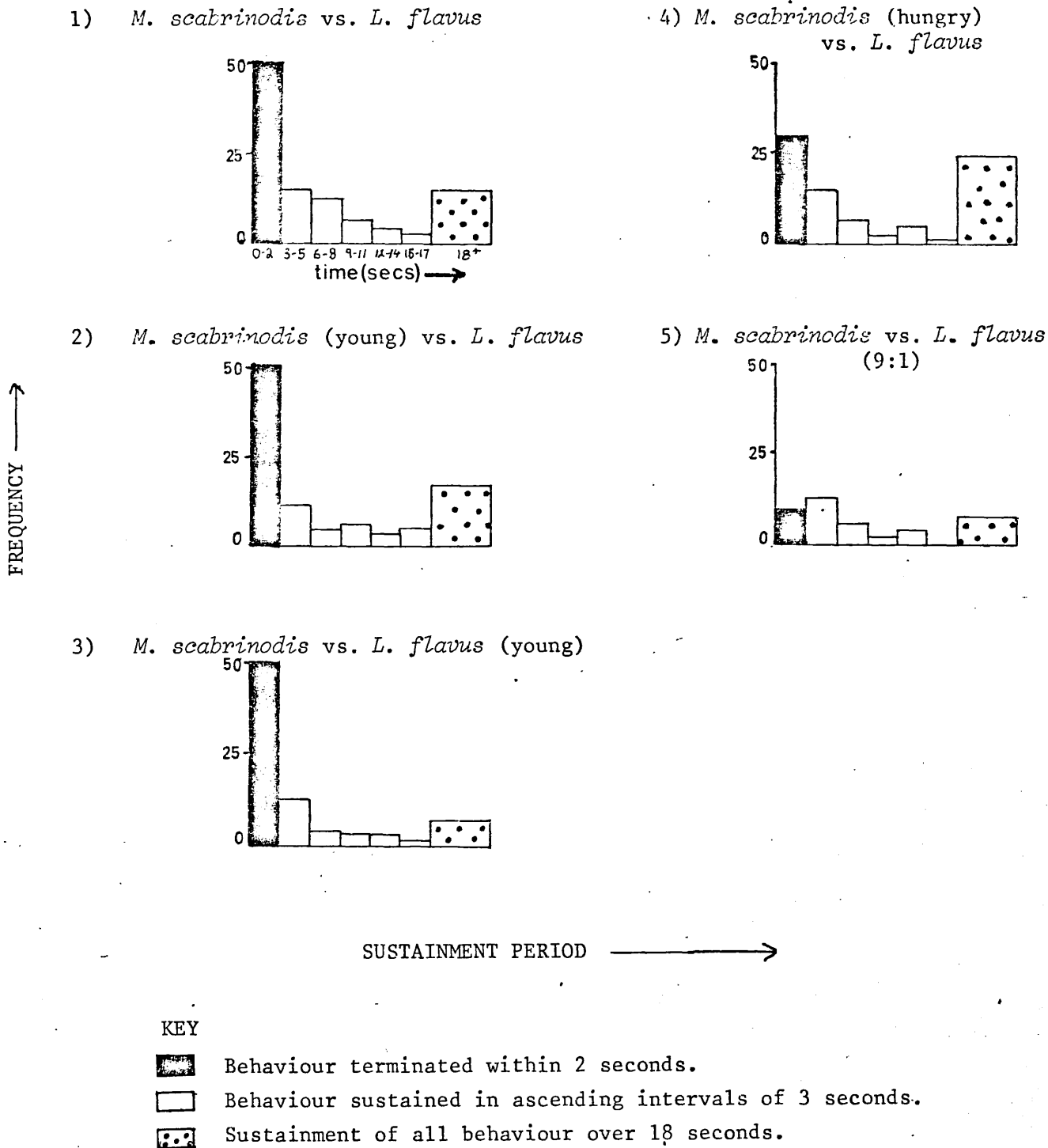
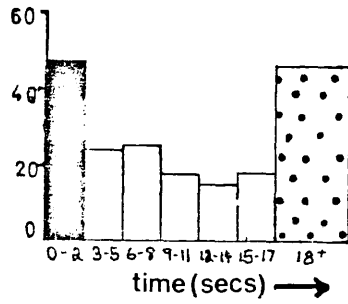
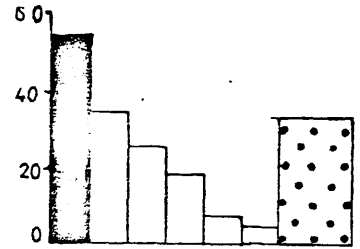


FIGURE 4 Sustainment of the STILL response by *M. scabrinodis* after a meeting with *L. flavus* in 5 types of experimental encounters.

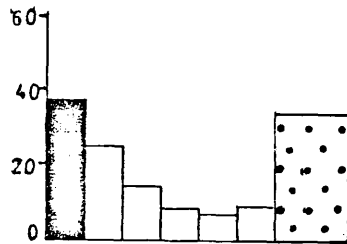
1) *M. scabrinodis* vs. *L. flavus*



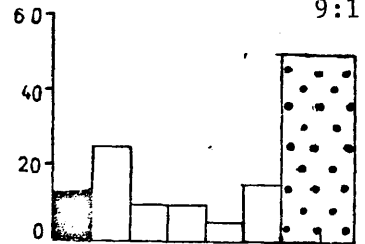
4) *M. scabrinodis* (hungry) vs. *L. flavus*.



2) *M. scabrinodis* (young) vs. *L. flavus*



5) *M. scabrinodis* vs. *L. flavus* 9:1

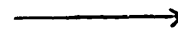


3) *M. scabrinodis* vs. *L. flavus* (young)



FREQUENCY

SUSTAINMENT PERIOD



KEY



Behaviour terminated within 2 seconds.



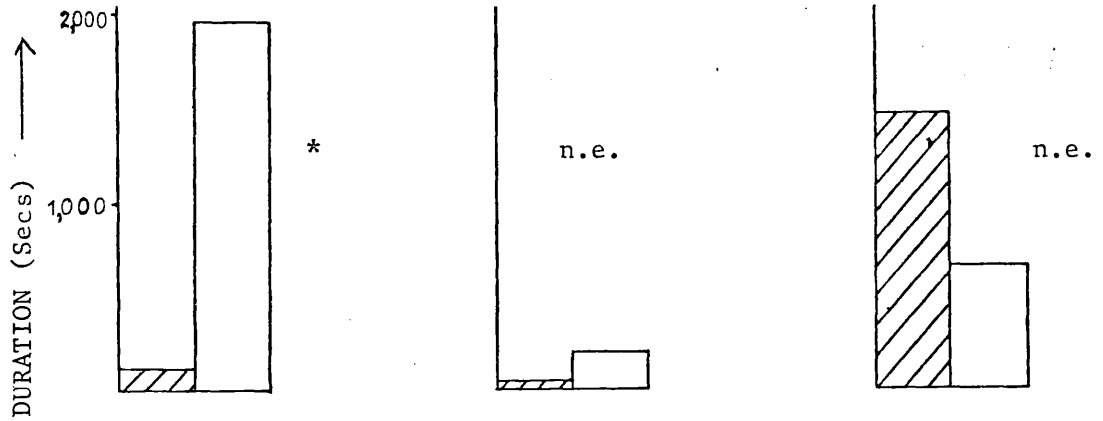
Behaviour sustained in ascending intervals of 3 seconds.



Sustainment of all behaviour over 18 seconds.

FIGURE 5. Sustainment of the ABDOMEN CURLING response by *M. scabrinodis* after a meeting with *L. flavus* in 5 types of experimental pair encounters.

- 1) *M. scabrinodis* vs. *L. flavus*      2) *M. scabrinodis* (young) vs. *L. flavus*      3) *M. scabrinodis* vs. *L. flavus* (young)



- 4) *M. scabrinodis* (hungry) vs. *L. flavus* - little CONFLICT shown.  
5) *M. scabrinodis* vs. *L. flavus* (9:1) - CONFLICT not examined.

KEY



MEET PERIOD



INTERMEET PERIOD

\*

P<0.05

n.e.

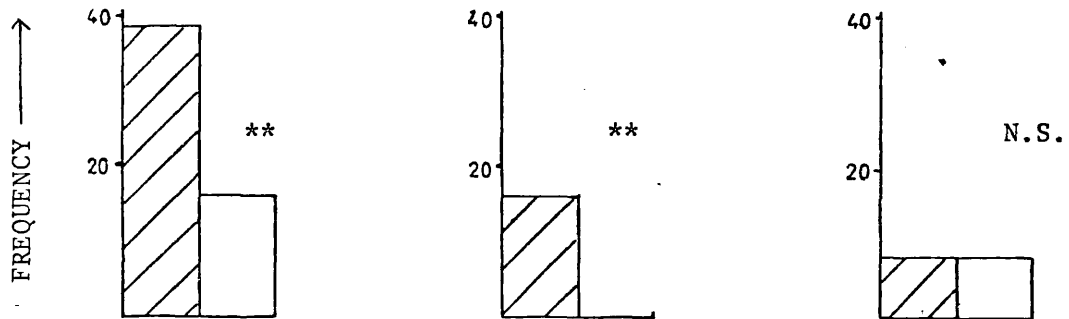
not examined, sample size too small.

FIGURE 6. Comparison of the CONFLICT response performed in the MEET and INTERMEET periods by *M. scabrinodis* in 4 different types of pair encounters.

a) *M. scabrinodis* vs. *L. flavus*

b) *M. scabrinodis* (young) vs. *L. flavus*


c) *M. scabrinodis* vs. *L. flavus* (young)




d) *M. scabrinodis* vs. *L. flavus* - little CONFLICT shown.

e) *M. scabrinodis* vs. *L. flavus* (9:1) - CONFLICT not examined.

KEY

 Behaviour terminated immediately.

 Behaviour sustained.

N.S. Not significant

\*\*  $p < 0.01$

FIGURE 7. Termination/sustainment of the CONFLICT response shown by *M. scabrinodis* when confronted by the opponent, *L. flavus* in 4 types of pair encounter.

values slightly above the 5% significance level.

### 2.3. Interactions between colonies.

#### 2.3.1. The behaviour of *M. scabrinodis* to prey in laboratory and field conditions.

##### (i) Introduction and Method.

The previous experiment showed that *M. scabrinodis* will attack and carry dead *L. flavus* workers. The same behaviour has been noted in the field. The following experiment investigates the behaviour of *M. scabrinodis* to 3 types of prey: dead *L. flavus*, dead *Drosophila* adults and *L. flavus* pupae. The main aims of this simple experiment were to establish whether or not *M. scabrinodis* will retrieve *L. flavus* corpses to its nest and eat them and also to examine any obvious food preferences of the ant. Some ants will, when given a choice, show a preference for certain food items (Ayre, 1963), and most species will readily take 'foreign' ant larvae back into their nest.

Five of each prey item were placed (i) in the foraging area of a laboratory colony and (ii) on top of a natural nest in the field. The behaviour of the ants to the prey was observed and notes were taken where appropriate. 3 trials were performed.

##### (ii) Results.

Workers of *M. scabrinodis* seized all 3 prey items and retrieved them to the nest, in both the laboratory and in the field, with seemingly no preference for a particular item. In the laboratory nest, dead prey were quickly dismembered by a number of individuals and readily eaten. Pupal cases were also quickly removed and their contents consumed. Most but not every worker carried back prey and occasionally more than one ant was involved in the retrieval.



2.3.2. Interactions between colonies of *M. scabrinodis* and *L. flavus* in the foraging areas of laboratory colonies.

(i) Introduction and Method.

In most of the previous experiments, interaction between the 2 species were studied with individuals and in a neutral area — the experimental arena. The following experiment was performed to investigate interactions between colonies of each species in a shared, or common, foraging area where factors such as chemical deposition, number of individuals and motivational state of the ants were all variable.

Laboratory housed nests of *L. flavus* and *M. scabrinodis* were taken and their foraging areas were connected by a piece of transparent plastic tube, so that each species had access to both foraging areas. The colonies were maintained as described in Section 2.2.

Experiments were performed with 2 different-sized colonies of *L. flavus*. The first consisted of some 500 workers, a queen and brood. This colony was then 'boosted' by the addition of approximately 1,500 more workers for the second experiment. The colony of *M. scabrinodis* was the same in both experiments and comprised approximately 150 workers, 2 queens and their brood.

Interactions between workers of the 2 species were observed in the foraging areas for a period of about 3 weeks and behavioural notes taken where appropriate.

(ii) Results

a) Interactions with a relatively small nest of *L. flavus*.

Workers of each species were soon seen in both foraging areas. The behaviour of the *Myrmica* towards the *Lasius* at the former's nest entrance was variable. Some red ants showed aggression by immediately

seizing, stinging, and dragging the enemy back into the nest. Other ants approached but became motionless, performing the STILL and ABDOMEN-CURLING responses. A third type ran hurriedly to and from the nest; workers inside became excited and soon emerged. A *Lasius* was invariably released from the 'grips' of a *Myrmica* if it managed a counter-attack, particularly when the gaster was used. This occurred many times.

Interactions often took place between single individuals away from the nest entrances. The behaviour here was very similar to that seen in 'pair encounter' experiments. *L. flavus* approached quickly and rigorously inspected the red ant and showed much aggression. The *Myrmica* became motionless as before by performing the STILL and ABDOMEN-CURLING responses. The 'passive' postures were often sustained after the *Lasius* worker had departed, again as in pair encounter experiments. Fighting did not occur and both ants were always uninjured.

The *Myrmica* performed the same behaviour when surrounded and attacked by several *Lasius*. The posture was sustained, as before, and the red ant performed locomotion afterwards in a 'normal' unhurried manner. *M. scabrinodis* were attracted to the *Lasius* workers and occasionally several of them became grouped around a single *Lasius*. This was particularly noticeable around the *Myrmica*'s nest entrance. The behaviour here was very similar to that in the 'numbers' experiment within the experimental arena. The approach was slow and any THREAT, CONFLICT or other movements were inhibited by the contact inspection of *L. flavus*. No further aggression was shown and the ABDOMEN-CURLING and STILL postures were adopted as before. The *L. flavus* worker eventually departed, uninjured.

Interactions frequently occurred at the food site. The behaviour of both ants was essentially the same as above. If *M. scabrinodis* was challenged while carrying prey back to the nest, it became motionless

and sometimes performed ABDOMEN-CURLING, but in each case maintained its grip on the prey item.

Individual workers of *M. scabrinodis* were often seen to approach and remain around the *Lasius* nest entrance. They did not display aggression when challenged but again performed and sustained the passive postures. At times, many *Myrmica* could be seen motionless in this region, 'side by side' and oriented towards the entrance. They were able to remain here uninjured.

Throughout the experiment, fewer and fewer *L. flavus* ventured out into their own foraging area. Indeed, at one point several *M. scabrinodis* entered the tube leading from the foraging area into the *L. flavus* nest. An unusual piece of behaviour was seen when *M. scabrinodis* carried corpses of their own colony and placed them in a semi-circle around the opponents' nest entrance. These corpses were moved aside, several times, by the 'experimenter' and on each occasion they were replaced by the red ants. The *Myrmica* was obviously restricting the freedom of its opponent although none of the latter were seen to be killed or carried back to the nest (with the exception of the initial interactions at the red ants' nest entrance). The *Lasius* colony was in fact, prevented from entering and feeding in the foraging area for a long period of time.

b) Interactions with a relatively large nest of *L. flavus*.

By increasing the size of the *Lasius* colony, the number of *L. flavus* entering the foraging areas increased. Consequently, most interactions between the species involved several *L. flavus* workers attacking each *M. scabrinodis*. The behaviour was essentially the same as before: *L. flavus* displayed aggression and *M. scabrinodis* behaved submissively and no fighting took place. As *L. flavus* increased in numbers in the

foraging area, the red ants progressively retreated to a small area around their own entrance. Here soil was collected and piled up - a behaviour they did not do when with the small colony of *L. flavus*! Around the nest entrance and in the connecting tube leading to the nest the ABDOMEN-CURLING postures were again adopted and no aggression was shown. *L. flavus* continued to advance and attack the *Myrmica* nest and eventually they succeeded in entering it. The *Myrmica* soon fled from their own nest.

2.3.3. Interactions between colonies of *M. scabrinodis* and *L. flavus* inside an artificial 'compound' nest.

(i) Introduction and Method.

The 2 species are, as stated, often found living together in the same *Lasius* nest mound. Previous experiments showed that *M. scabrinodis* are not only attracted to *L. flavus* individuals but will also try to gain entry into their nest. The following experiment was devised to examine the invasion behaviour of *M. scabrinodis* into an artificial nest occupied by *L. flavus* and then to observe interactions between the species there.

The animals used in this experiment consisted of a colony of *L. flavus* of approximately 4,000 workers, 3 queens and brood, and a colony of *M. scabrinodis* comprising 200 workers, 5 queens and brood.

A large artificial nest of plaster (45cm x 45cm) was constructed to house both species and it was in this that interactions between the colonies took place. The quarters for *L. flavus* occupied most of the nest while *M. scabrinodis* was designated a small area (15cm x 15cm) at one corner. The nests were separated by plaster walls except for a region 10cm in length. Here, a movable wire gauze partition, with 0.5mm mesh, was inserted. This was thought necessary to separate the 2 nests initially until the ants were established - hostility between the 2 species has been adequately demonstrated in previous experiments.

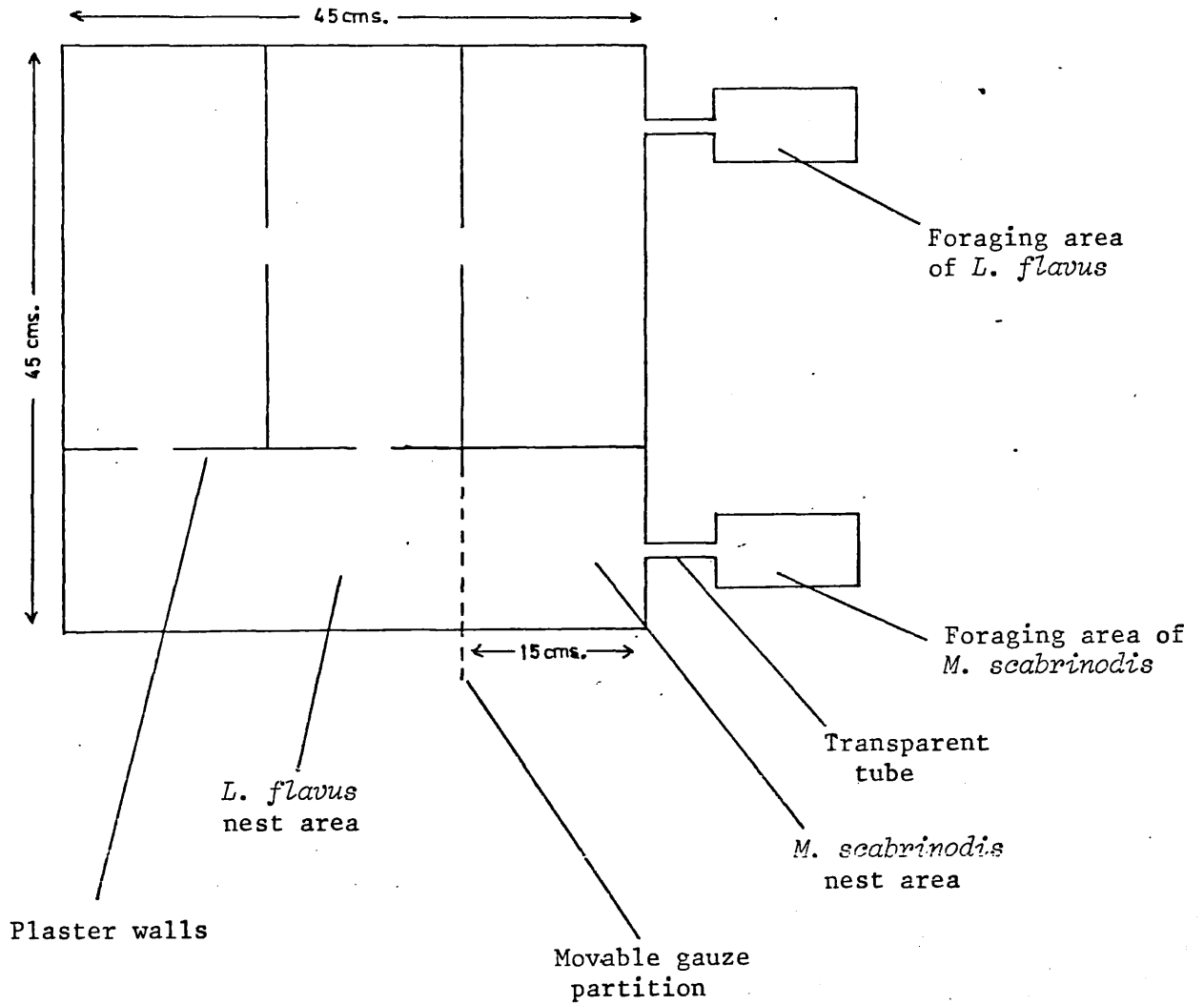


FIGURE 8. Plan of the experimental plaster nest designed for interactions between colonies of *M. scabrinodis* and *L. flavus*.

Each colony had a separate foraging area into which a small amount of soil, c. 15gm , was placed. The apparatus is illustrated in Figure 8 . The ants were introduced into the nests via their respective foraging areas. *L. flavus* was allowed to enter 3 days before its opponents. Preliminary experiments showed that although the wire gauze prevented the passage of most individuals, a number could, and would, get past it. After 3 more days the gauze was removed allowing free access of both species to both nests. The behaviour of *M. scabrinodis*, on entering the nest, towards the *L. flavus* and ensuing interactions between the species was observed, at intervals, over a period of 10 days. Where appropriate, notes were made, the general location of animals was recorded on diagrams, and photographs were taken. The experiment was repeated 3 times.

(ii) Results.

a) Interaction between the two species with the partition separating the 2 nests.

The first workers of *M. scabrinodis* entering the nest were confronted with workers of *L. flavus*. Approximately 30 *L. flavus* workers had gained access to the *Myrmica* nest area via the partition. These *L. flavus* immediately approached and attacked them. The *Myrmica* assumed the STILL and ABDOMEN-CURLING postures and showed little aggression; no fighting took place (see Plate 9 ). The red ants remained relatively inactive around the nest entrance while the majority of the colony stayed in the foraging area. *M. scabrinodis* crept forward very gradually, but assumed the passive postures each time they came into contact with the enemy. Eventually, all the colony had entered the nest. Whilst most of the colony remained near to the entrance, some workers advanced further into the nest and towards the opponents. The *Myrmica* workers moved forward very slowly, in distinct rows and side-by-side. On meeting a *L. flavus* worker, the passive postures were displayed and often sus-



PLATE 9. 'Passive' responses shown by *M. scabrinodis* on entering  
a nest occupied by *L. flavus*.



PLATE 10



PLATE 11

PLATES 10 and 11. 'Passive' responses employed by *M. scabrinodis* to gain ownership of nest territory of *L. flavus*.



tained for long periods after the opponent had departed (see Plates 10 and 11). A row of *M. scabrinodis* was often seen motionless, in the absence of any opponents. *L. flavus* continued attacking ants in the column but as the *Myrmica* advanced so they retreated (see Figure 9 ). The red ants moved more freely behind their 'line of attack'. A *Lasius* worker sometimes passed into the area near the brood and attacked *M. scabrinodis* there. *M. scabrinodis* on being attacked behaved 'passively', but as workers moved more freely there *L. flavus* was invariably surrounded by a group of opponents (see Plate 8 ). The grouping behaviour by *M. scabrinodis* around the enemy was essentially the same as that seen in experiment 2.2.4 in the experimental arena. Ants surrounding *L. flavus* assumed the 'passive' postures while the latter showed much aggression. After a short while *L. flavus* left the interaction uninjured.

The 'columns' of *Myrmica* continued moving towards the gauze partition separating the 2 nests and after 2 hours all *L. flavus* individuals were confined to areas near this gauze partition. *M. scabrinodis* were positioned closely, side by side, directly in front of them. After four hours, the opponents were closely confined to an area by the partition at "D" (see Figure 10 ). The *Lasius* were completely enclosed by a dense wall of *Myrmica* bodies. Almost all the *Myrmica* performed the ABDOMEN-CURLING posture in this interaction and while some stood on top of their sisters others were suspended from the roof. The *Lasius* continued to show aggression. At other places along the partition, where no *Lasius* were present, a single row of *M. scabrinodis* remained. Within the nest, the *Myrmica* colony showed an increase in activity and the queen and brood were seen away from the nest entrance for the first time. After 24 hours few *L. flavus* were to be found at the gauze partition but the single row of ants along each part of it remained (Figure 10 illustrates the relative position of ants at this time). Elsewhere in the nest, 4 *Lasius* were dead and 3 others were

being attacked ( Plate 12 ). Both dead and live *L. flavus* were observed in the foraging area. Many *Myrmica* were active in the foraging area and much soil was carried into the nest and deposited on and near the gauze partition.

The workers that advanced in columns and engaged in interactions with *L. flavus* at the gauze partition were thought to be chiefly of the oldest pigmentary group. To test this the workers that were present in columns at the gauze were observed twice a day (at 10.00h and at 16.00h) for 5 days and placed into their respective pigmentary groups. (See Section 3.3.3.9), page 11) The following Table clearly shows that the workers involved in this activity belonged predominantly to the darkest melanic group.

TABLE 25. Number of workers of 5 pigmentary (ethal) groups of *M. scabrinodis* present at places of interaction with *L. flavus* and performing 'passive' responses.

MELANIC GROUP	1	2	3	4	5
FREQUENCY TOTAL	0	0	1	11	77

After 3 days no live *Lasius* were to be found inside the *Myrmica* nest. *Myrmica* workers formed rows along the gauze and remained there as before.

b) Interactions between the two species with the partition removed.

When the wire partition was removed at 'D' both species were attracted to the area in numbers. *M. scabrinodis* quickly showed the 'blocking' behaviour, seen before, by performing the ABDOMEN-CURLING postures in compact rows. By doing this activity, the *Myrmica* succeeded in sealing up much of the newly-created gap between the two nests for several hours. *L. flavus* attacked their opponents fiercely and some eventually managed to pass through the 'wall'. Many *Myrmica* brought



soil into the nest from the foraging area. Some soil was deposited at the region of interaction at 'D' but most was placed around the nest entrance. A wall of soil was constructed around the entrance. Many *L. flavus* gained entry into the nest before the soil wall had been completed and congregated in regions where gaps existed. The relative position of the ants and the wall is illustrated in Figure 11. *M. scabrinodis* again assembled and performed the 'blocking' activity at the spaces in the wall. Where the 'gap' was small a single worker was present, exhibiting the ABDOMEN-CURLING posture. *L. flavus* continued to attack the red ants throughout the nest and some gained entry via the gaps in the wall, into the 'new' nest area of the enemy. While *Myrmica* outside the soil wall behaved 'passively' in interactions with *L. flavus*, those meeting *L. flavus* inside the nest seized and killed them. After many hours the soil wall was complete. *Myrmica* workers throughout the study were often observed outside the wall - i.e. in the nest territory now possessed by *L. flavus*. Here they were seen carrying soil and 'repairing' the wall. The *Myrmica* ceased its duties and behaved passively when attacked by *L. flavus*. *L. flavus* were very aggressive towards the opponents encountered outside the wall and many were seized and dragged away from this area, through the *Lasius* nest and deposited in the *L. flavus* foraging area. *Myrmica* workers, found in the foraging area of *L. flavus*, were collected and placed into groups according to the degree of cuticle pigmentation (see Section 3. 3.3.9) page 11). The frequency of workers in each group is given in the following table:-

TABLE 26. The number of *M. scabrinodis* workers of 5 pigmentary groups found in the foraging area of *L. flavus*.

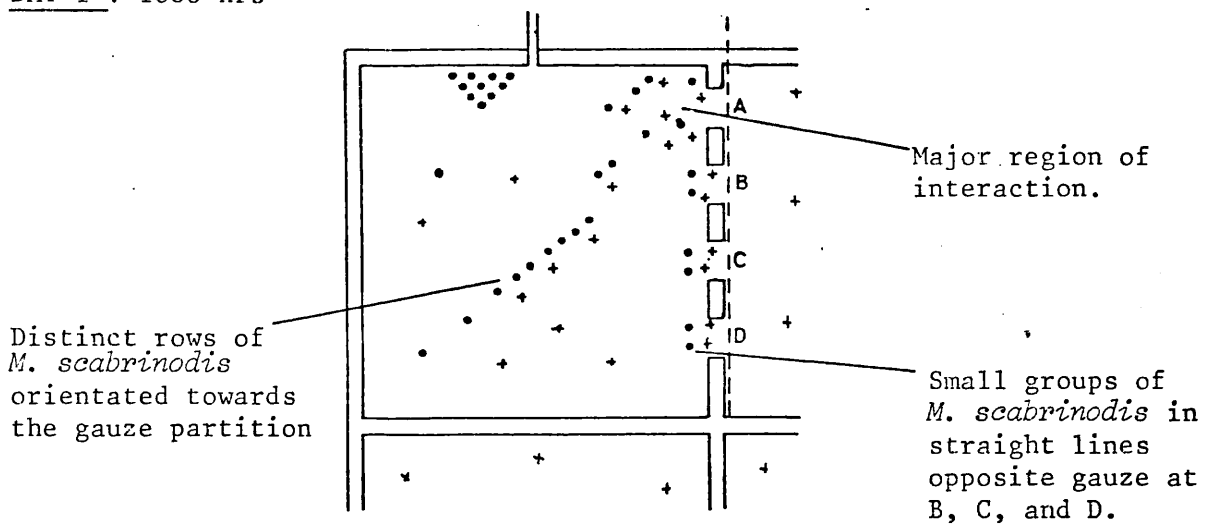
MELANIC GROUP	1	2	3	4	5
FREQUENCY	0	0	4	56	24

Some of the *Myrmica* workers found in the *L. flavus* foraging area were alive and apparently healthy, although others were dead. *L. flavus*

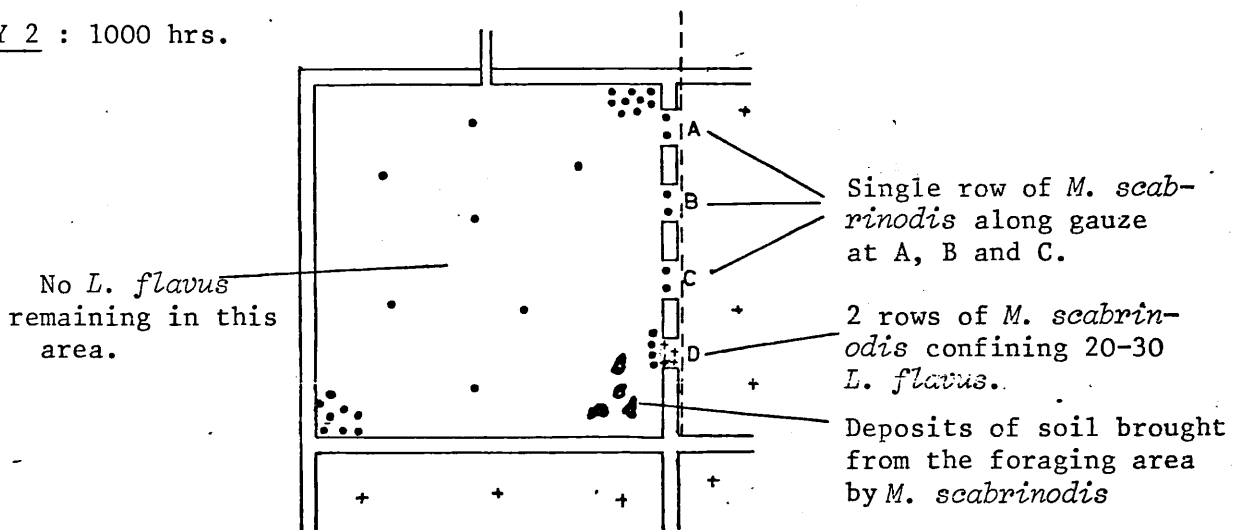
Key to FIGURES 9 - 14

- A, B, C, D.    Regions between the 2 areas of the compound nest separated by a gauze partition.
- Relative position of *M. scabrinodis* individuals.
- +                Relative position of *L. flavus* individuals.
-                 Position of the queen, brood and concentration of *Myrmica* workers.
- • • •                Distinct rows of stationary *M. scabrinodis* performing STILL and ABDOMEN CURLING responses.
-                 Soil walls built by the ants during the experiment.

DAY 1 : 1000 hrs

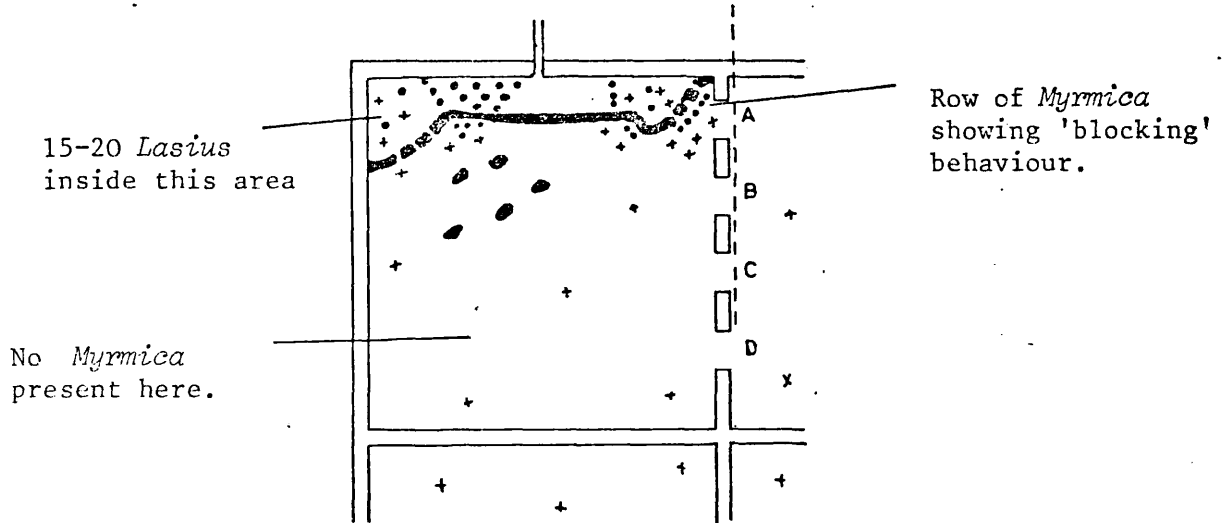


DAY 2 : 1000 hrs.

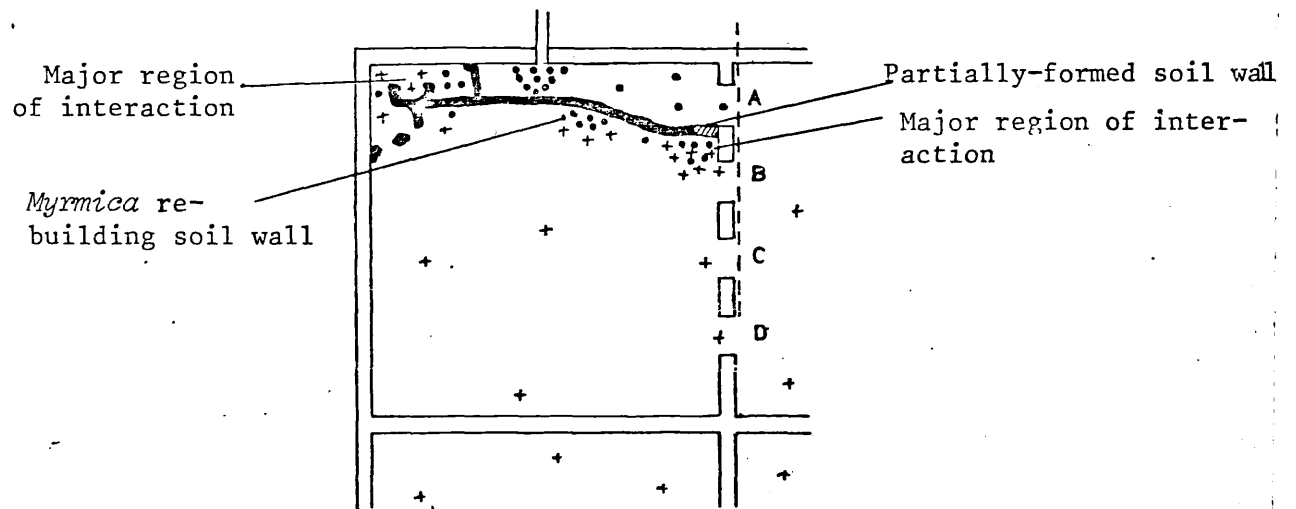


FIGURES 9 AND 10. Relative position of 2 species of ant at various times after the invasion by *M. scabrinodis* into the artificial nest occupied by *L. flavus* (see KEY opposite).

DAY 5 : 1000 hrs.

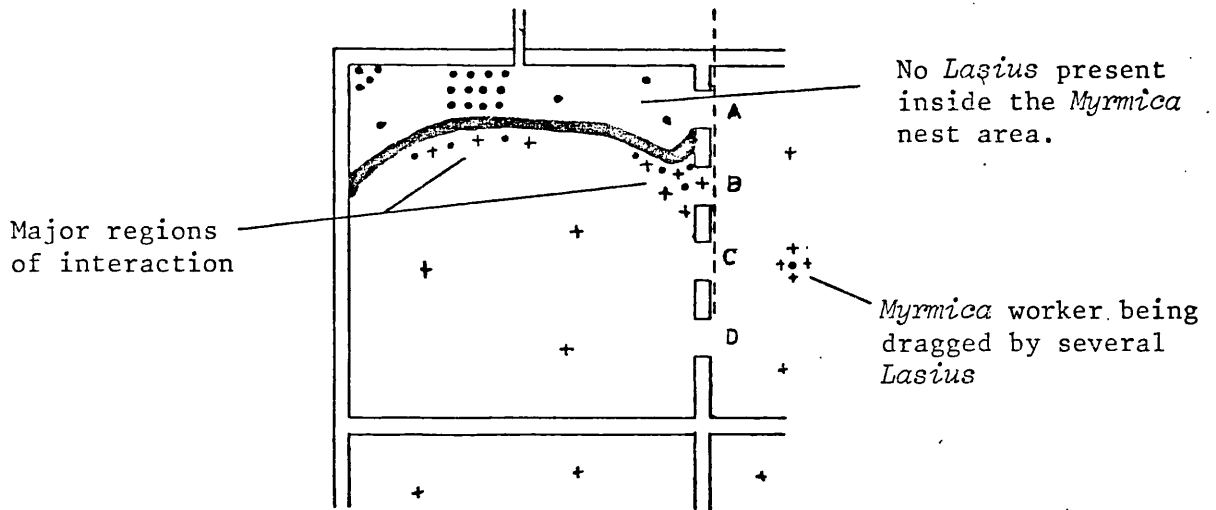


DAY 5 : 1800 hrs.

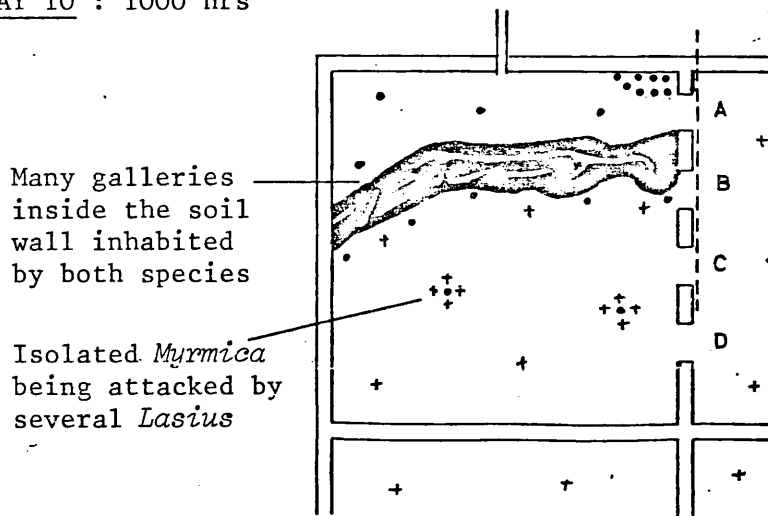


FIGURES 11 and 12. The relative position of interacting colonies of *M. scabrinodis* and *L. flavus*, and the building of soil walls in an artificial compound nest. (see KEY).

DAY 7 : 1000 hrs



DAY 10 : 1000 hrs



FIGURES 13 and 14. Relative position of interacting colonies of *M. scabrinodis* and *L. flavus*, and of soil walls in an artificial compound nest. (See Key).

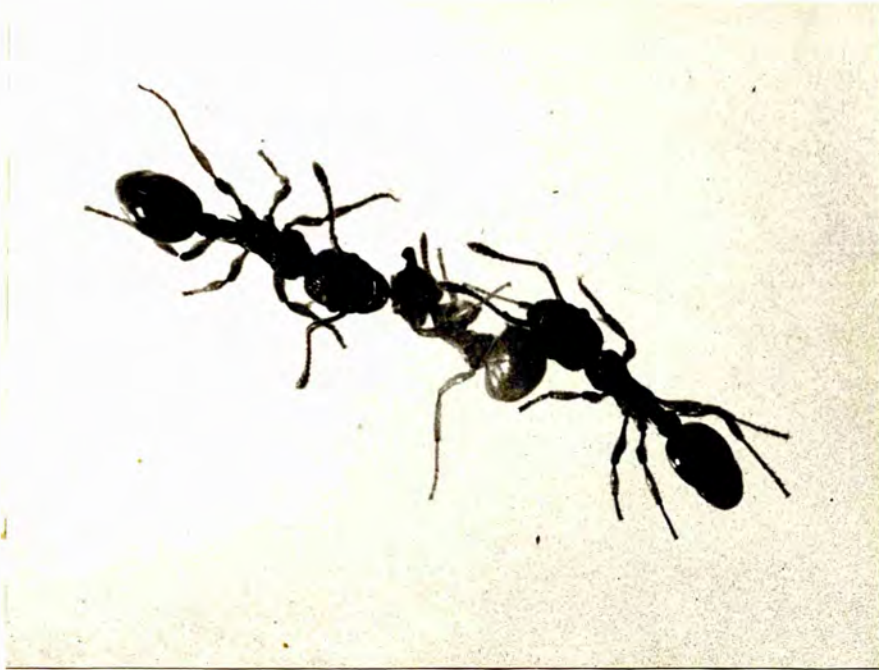


PLATE 12. Two *M. scabrinodis* workers attacking a solitary *L. flavus*.

L. flavus invading the Myrmica nest.



PLATE 13. Artificial soil compound nest of *M. scabrinodis* and *L. flavus*.



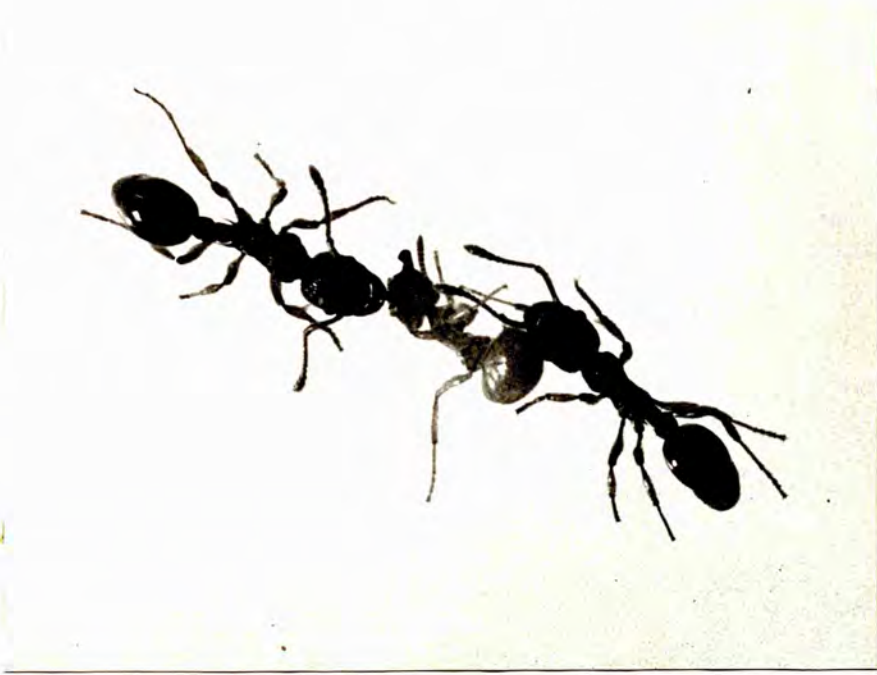


PLATE 12. Two *M. scabrinodis* workers attacking a solitary *L. flavus*.



PLATE 13. Artificial soil compound nest of *M. scabrinodis* and *L. flavus*.

workers persisted in trying to gain access into the *Myrmica* nest throughout the experiment, by removing soil from the wall. When the wall was penetrated by *L. flavus*, *M. scabrinodis* assembled in numbers at that point and performed its 'blocking' behaviour. The *Myrmica* were successful in either reforming the wall or in building another one at some distance behind the gap. The change in the position of the soil wall can be seen in Figures 12 and 13. Where a new wall was constructed, the *Myrmica* involved in the 'blocking' behaviour appeared to be 'stranded' outside their nest!

Once the soil wall was firmly established, the *Myrmica* workers added to its thickness. Galleries became visible within the wall and interactions between the two species occurred within them. Single workers of *L. flavus* occasionally gained access to the *Myrmica* nest and here they were seized and killed (see Figure 14).

#### 2.3.4. Interactions between colonies of *M. scabrinodis* and *L. flavus* in an artificial soil nest.

##### (i) Introduction and Method.

The previous experiment showed that it was necessary for *M. scabrinodis* to build soil walls as a protection against the aggressive *L. flavus* in the artificial compound nest. The following experiment was performed to investigate the building activities of the ants in more detail and their importance in the <sup>co-</sup>existence.

The behaviour of *M. scabrinodis* and *L. flavus* was investigated in an artificial soil nest. The observation nest consisted of a layer of moist, sandy soil, 0.5cm deep, between two sheets of window glass, 38 x 23 x 0.3cm. A thin strip of cork was stuck between the glass around the edges to seal in the contents. Two plastic foraging areas were connected to opposite ends of the nest as shown in Figure 15.

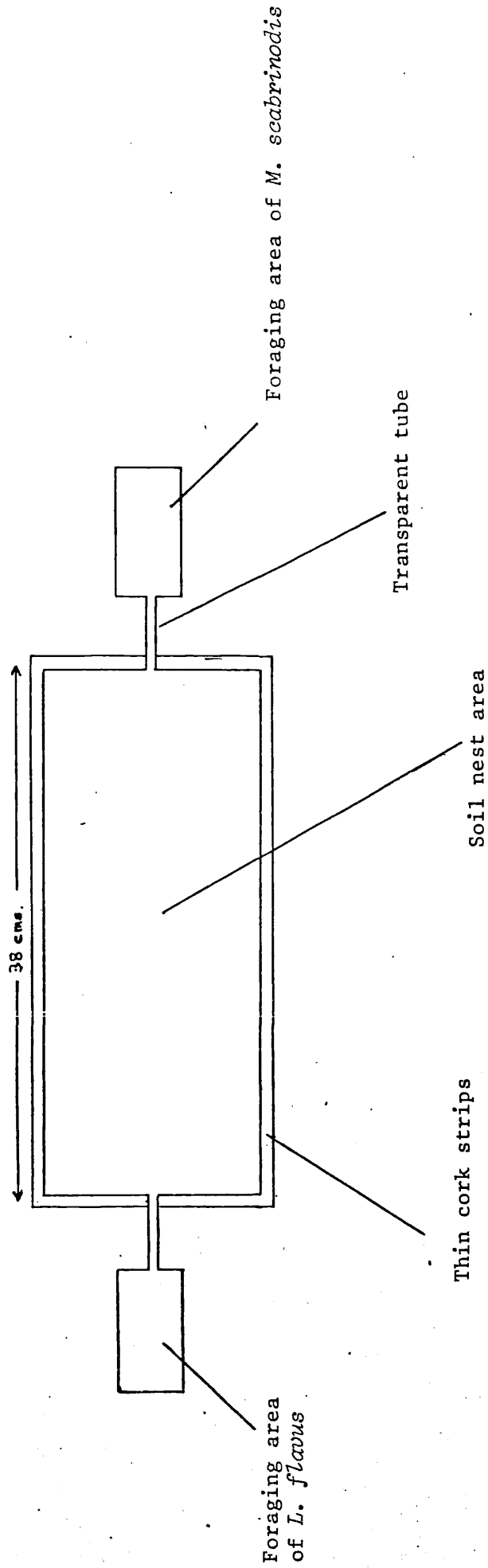


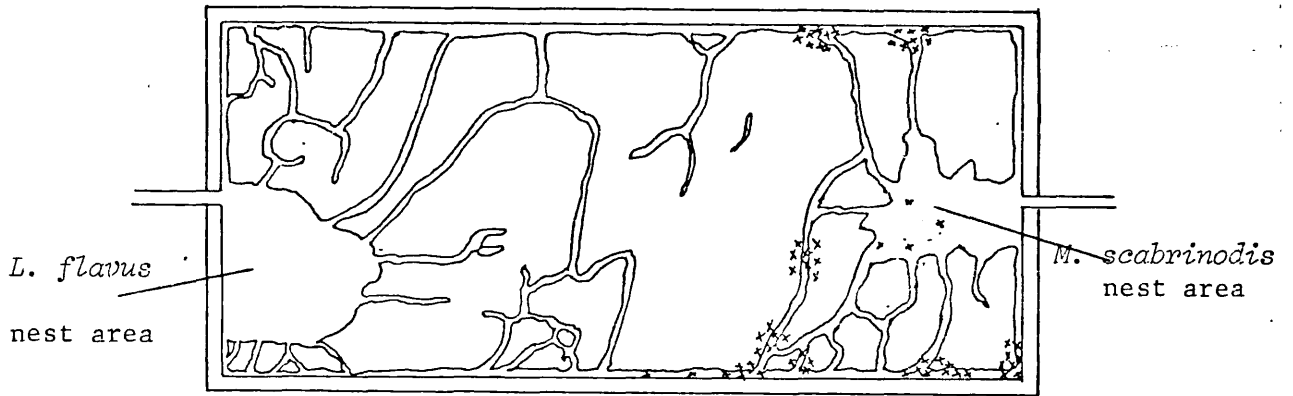
FIGURE 15. Artificial soil nest.

The nest was designed so that construction of chambers and galleries by the ants would effectively give two dimensions and thus aid observations. Colonies of *L. flavus*, c. 1,000 workers, 1 queen and brood, and *M. scabrinodis*, c. 200 workers, 2 queens and brood, were each placed in a separate foraging area and allowed to enter the artificial soil nest. (The ants were fed and maintained as in Section 2.2). Behaviour of the ants in the nest and interactions between the species was observed at intervals for a period of 10 days. Where appropriate, notes, diagrams and photographs were taken. The experiment was repeated 3 times.

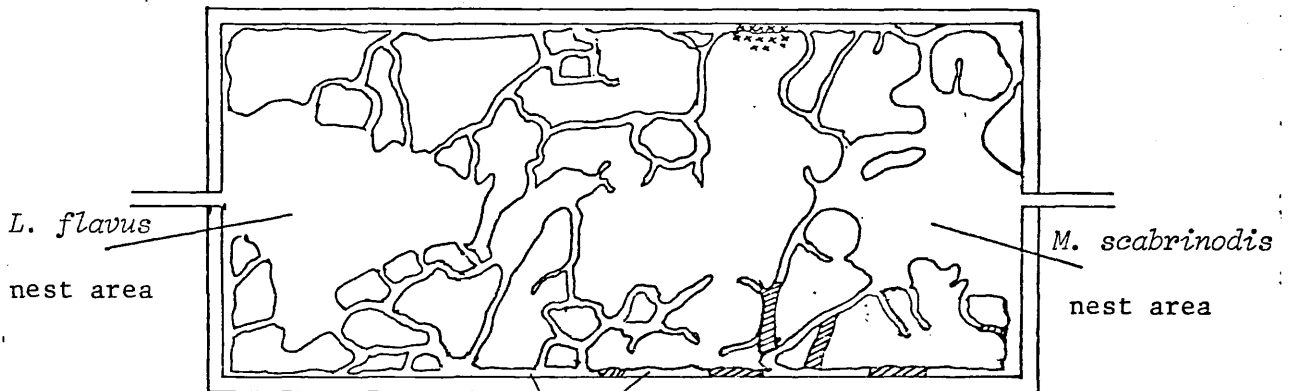
(ii) Results.

Both species entered the artificial nest and, by excavating soil, constructed chambers and galleries there. The queens and brood were soon found in the nest. Galleries were extended deep into the nest by both species. The galleries were constructed most quickly around the sides of the nest and it was at the perimeter where the two species first met (see Figure 16 (1)). On meeting, *L. flavus* attacked the opponents showing much biting and seizing. Many *L. flavus* were recruited to the area, engaged in the attack and tried to gain access into the enemy's nest. *Myrmica* workers also convened at the places of interaction and performed their STILL and ABDOMEN-CURLING behaviour. A 'blocking' effect, similar to that seen in the previous experiment, was produced which restricted the passage of *L. flavus* workers at those places. Aggression was seen in some of the *Myrmica* workers, fighting occurred, and both *Myrmica* and *Lasius* were killed. Other *Myrmica* collected soil and built barriers at the places of interaction. Often, bodies of *L. flavus* were incorporated by *M. scabrinodis* in the barrier! Although *L. flavus* persisted in trying to enter the *Myrmica* nest area the latter succeeded, on day 4, in completing the barriers so that no more *L. flavus* could enter their nest. Some *Myrmica* workers were

1) DAY 3



2) DAY 7



*Myrmica* workers isolated from their nest  
by soil barriers and attacked by *L. flavus*.



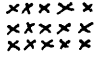

- KEY.
-  Galleries
  -  Nest chambers.
  -  Regions of interaction between the 2 species.
  -  Soil barriers constructed in existing galleries by *M. scabrinodis*.

FIGURE 16. Relative position of chambers and galleries constructed by *M. scabrinodis* and *L. flavus* and regions of interaction between the 2 species on an artificial compound soil nest.

seen, on completion of the barriers, to be left 'stranded' on the inside of their nest in the *L. flavus* territory. Their fate was not determined. Further building activity was seen in the galleries which were sometimes completely 'filled in' for some distance and their course redirected (see Figure 16(2)). A number of *L. flavus* (approximately 50) did succeed in entering the *Myrmica* nest area, before the barriers were made, where they continued to behave aggressively. Some of these intruders were seized and killed while others moved freely in the nest for some time. By day 7 (Figure 16,2) all the *Lasius* had been removed from the nest to the foraging area and many were dead. Bodies of *Myrmica* were also seen there.

The *L. flavus* colony continued to extend its nest area and by doing so its galleries again came into contact with the opponents' nest. The behaviour of each species was essentially the same as before. However, on one occasion the *Lasius* entered the opponents' nest in large numbers and the *Myrmica* were unable to stop their entry. After a short while the *Myrmica* were forced out of the nest into the foraging area. The *Myrmica* were overwhelmed and so the experiment was stopped.

When the experiment was repeated, a similar pattern of events took place. On one occasion the *Myrmica* colony remained in the nest throughout the 10 day period; in the other two experiments the colony evacuated the nest area and fled into the foraging area.

#### 2.3.5. Observations on a naturally-occurring compound nest of

*M. scabrinodis* and *L. flavus*.

##### (i) Introduction and Method.

The 2 species were hostile to each other in artificial compound soil nests in the laboratory. Changes in the relative position and ownership of the nest areas were seen. A naturally-occurring compound nest was therefore observed in the field over a summer period to examine

further the spatial nesting relationship of the species.

The compound nest examined was present in a *L. flavus* mound. A concrete slab ( 20 x 20cm) had been placed on top of this nest the previous year. Ants congregate under these slabs, presumably for the warmth, and can, therefore, be easily collected. A glass plate ( 19 x 19cm ) was placed beneath this slab. By removing the slab, when required, the ants under the glass could be observed - the only disturbance was therefore that of light. After instalment of the 'glass window' the ants were allowed 1 week to readjust before observations began. The location of the 2 species and of their galleries beneath the glass was observed at intervals over a 6 week period. Notes and diagrams were taken where appropriate.

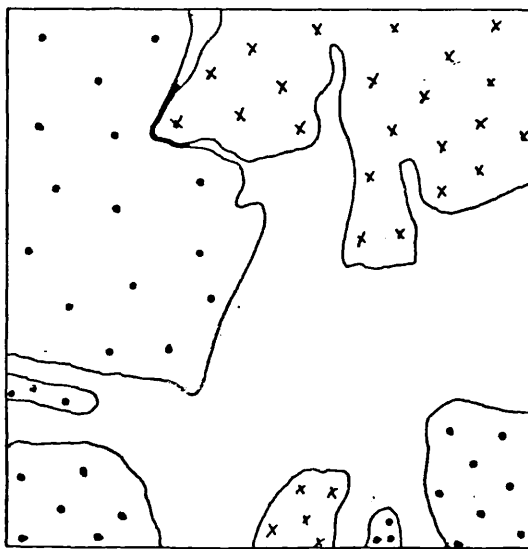
(ii) Results.

Both *M. scabrinodis* and *L. flavus* were present in large numbers beneath the glass. Each species occupied separate quarters. The relative position and occupation of galleries initially and after 6 weeks are illustrated in Figures 17(1) and (2). It can be seen that some changes in number, shape, position and ownership of chambers did occur over the observation period. However, the two main areas occupied by each species remained essentially the same. Soil separating adjacent chambers of the species was very thin in places. The positions of these 'soil walls' were not constant. No corpses or live individuals of one species were seen in the other species nest area, except on one occasion. Light, entering the nest during observations, caused some excitement in the ants. This factor was thought to be responsible for the invasion at this time. The *Myrmica* were seen to enter the *L. flavus* area from a tunnel emerging from below. Interactions between the 2 species followed and some fighting occurred. At times, both species adopted and sustained a threatening posture a few millimetres from each other.

1) DAY 1



2) DAY 42



KEY



Areas of soil



Areas occupied by *M. scabrinodis*



Areas occupied by *L. flavus*



Thin soil walls separating the nests of the 2 species.

FIGURE 17 Relative position of the areas occupied by *M. scabrinodis* and *L. flavus* in a naturally occurring compound nest.



The *Myrmica* were also seen to perform and sustain their passive postures 'side by side'. The area was eventually regained by the *Lasius*.



PLATE 14      SCANING ELECTRON MICROGRAPH of the head of a *M. scabrinodis* worker. Points of particular interest are the labral hairs between the mandibles; the deep antennal pits and sharply bent scapes, and the heavy sculpturing of the head (  $\times 42$  ).

### 3. Discussion

The aggressiveness and behaviour of an ant are related, in part at least, to the physical characteristics of the species. *M. scabrinodis* and *L. flavus* differ in the colour, toughness and rugosity of the cuticle, size, eyesight and their defence systems. An examination of exploratory behaviour here shows that the 2 species differ greatly in their rate of locomotion - the speed of *L. flavus* is almost twice that of *scabrinodis*. The superior speed and manoeuvrability of *L. flavus* may have a significant beneficial influence in encounters with respect to both fighting and the rate of recruitment to zones of interaction. Both species explore an unfamiliar environment, i.e. the arena, in a similar way to one another. The high initial activity and subsequent decline is similar in pattern to that of cockroaches (Dorchen, 1952; 1955) and rats (Berlyne, 1960). The kind of persistent exploratory activity performed by these ants has been stated (Nissen, 1954; Thorpe, 1963) to be an important 'drive' to perceive and explore. Welker (1959) has pointed out that fear-induced tendencies may sometimes be produced by a forced trial. Ants will, by exploring, gain information of the environment and learn while doing so. *L. flavus* will thus gain information of a given area sooner than *M. scabrinodis*. Exploration has been shown to be a prominent and distinctive form of learning in vertebrates (Harlow *et al* 1954; Buttler, 1960) and true associative learning may take place. However, the learning systems are different between ants and vertebrates (Schnierla, 1959) and thus care should be taken in any comparison of the two. The difference in exploration between old and young animals is very pronounced. The young animals spend less time walking and more time grooming than older ones. In fact, older animals of the 2 species resemble each other more in this behaviour than they do young workers of their own species.

This is related to their foraging activity. Many authors (Buckingham, 1911; Ledoux, 1949; Wehr, 1958; Otto, 1958) have shown that older ants of some species tend to forage and are therefore found outside the nest while younger ones perform functions inside the nest. The detailed analysis of grooming in *M. scabrinodis* reflects this. The older animals, presumably more adept at foraging and exploration, perform only the necessary brief cleaning activities of the antennae while younger animals perform a wider variety of cleaning actions and, consequently, spend less time exploring.

Grooming behaviour has been used as an aid to classification and phylogenetic origin in social insects (see Farish, 1969 and Wilson, 1971). Both old and young *L. flavus* groom more than the respective age groups of *M. scabrinodis* but, for example, the grooming activity of young *M. scabrinodis* is higher and different in form from that of old *L. flavus*. Clearly, then, any comparisons of grooming behaviour must recognise not only quantitative and qualitative measures but also the type of 'individual' examined.

The motionless posture shown by *M. scabrinodis* in pair encounters is performed by a variety of animals in the wild when faced with danger. The term 'thanatosis' has been employed to describe such behaviour. Several ant species are known to show the response. Goetsch, (1953) reports the conciliatory posture of *Camponotus lateralis* on meeting a hostile *Crematogaster scutellaris* at a feeding ground. Kutter (1956, 1957) states that *Formica pressilabris* will 'play dead' and pull its appendages into the body when approached by an aggressor. Both *Leptothorax* and *Tetramorium caespitum* may show the response. Submissive postures are also used by parasitic queens in species such as *Formica exsecta*, *Epimyrma stumperi* and *Polyergus* to gain entry into the hostile host nest (see Wilson, 1971, Chapter 19).

Each time *M. scabrinodis* meets with and is attacked by *L. flavus* in pair encounters no fighting takes place. As the *Myrmica* is uninjured, even after 24 hours, the *Lasius* is either incapable, in a one to one situation, of injuring its opponent or is not using all the weapons at its disposal and to their fullest extent. The latter is almost certainly the case - *L. flavus* was not seen to seize or drag fiercely nor did it employ the gaster in attacks. The potent secretions and spreading agents of *L. flavus* have been described by Bergstrom and Lofquist (1972). *M. scabrinodis* is therefore not providing the stimuli, chemical or behavioural, needed to elicit a fierce attack. The motionless behaviour on meeting the aggressive *Lasius*, that is, the STILL and ABDOMEN-CURLING postures are functioning as aggression-reducing stimuli. Aggressive gestures are an effective stimulus for increasing the probability of attack (Marler and Hamilton, 1966) and these are absent in *M. scabrinodis*.

The elements of the 2 motionless postures resemble in many ways those of a typical submissive or appeasement display - the jaws are closed, the head is lowered and the antennae, usually active and essential for attack, are withdrawn close to the body and inside the prothoracic legs. Furthermore, a threat posture is erect whereas the body is low-slung in the STILL posture. The ABDOMEN-CURLING response has an elevated posture but here the tip of the gaster is placed firmly behind the jaws. Dominance hierarchies are thought to exist in *F. polyctena* (Lange, 1967) and in *Polistes* wasps (Montagner, 1966). Huber (1802) has pointed out that the dominant wasp adopts a high posture while the subordinate one crouches and withdraws its antennae. Some parasitic ant queens combine slow movement and submissive behaviour with antennal stroking in order to 'appease' hostile host workers. Study of the epidermal secondary gland system of *Termitella* has revealed the presence of an appeasement substance (Pasteel, 1969).

Jaison (1972) believes that young *F. polyctena* workers produce a substance that is effective in inhibiting the aggression of *M. rubra*. No indication of such a substance was observed in *M. scabrinodis*.

The apparent 'submissive' behaviour of *M. scabrinodis* gives no indication of the physiological or motivational state of the animal. The appeasement posture of birds and mammals, for example, is usually performed by an 'inferior' animal (Manning, 1972). In ants, the posture is often used (as stated above) as a ploy to reduce the opponent's aggression. What can be said is that the remarkably regular and stereotyped behaviour is a highly evolved mechanism which enables individuals to remain in an area uninjured, which might otherwise not be possible. Both of the submissive postures were often sustained after the *Lasius* had departed. This behaviour is also advantageous for reducing the aggression of the opponent as participant flight is known to be very effective stimulus for attack (Marler, 1956; Barlow, 1962).

The behaviour of *M. scabrinodis* individuals was similar in all kinds of pair-encounter experiments with *L. flavus*. However, the few responses that were performed when quantitatively compared reveal differences that are useful in understanding their function. The 3 responses STILL, ABDOMEN-CURLING and CONFLICT were performed most and are thus of particular interest.

One may first ask why either the STILL or the ABDOMEN-CURLING posture is shown in preference to the other (CONFLICT is shown with both postures). It is felt that the ant first performs the STILL posture and that the ABDOMEN-CURLING act is shown in response to a more fierce attack. The gaster is curled at once and sustained when several parts of the body, including the antennae and legs, are bitten.

The STILL posture was shown far more than the ABDOMEN-CURLING one in encounters with young *Lasius*, which are less aggressive than older ones. Further, the ABDOMEN-CURLING posture was shown much less in encounters with dead opponents than with live ones, while the STILL posture was shown in a similar way with both. If the posture is useful in some way in interactions with *L. flavus* one would expect older workers, because of maturation and experience, to show the behaviour more than young ones. This is, in fact the case. The behaviour, however, seems to have no observable advantage over the STILL posture in reducing *Lasius* aggression in pair encounters. Attacks on young and old *Myrmica* were considered to be similar and they lasted for similar durations (seen by comparing the MEET periods, as these are determined by the *Lasius*).

The ABDOMEN-CURLING posture is employed during colony interactions inside the nest—for example, by individuals and groups in blocking behaviour. The posture, therefore, contains most of the submissive elements of the STILL one but is modified for another purpose. A quantitative analysis of *L. flavus* aggression towards ants performing each of the 2 postures would evaluate the relative appeasement value of each more precisely.

CONFLICT is a term usually applied to vertebrates with respect to agonistic behaviour. It may also be applied to invertebrates. Studies of the octopus provide a good example (Young, 1961). Threatening behaviour is a form of CONFLICT and is believed to occur when attack and escape tendencies are present but cannot find separate expression (Manning, 1967). THREAT is a common response of ants. The CONFLICT response was used to describe the *Myrmica* behaviour because of the submissive and aggressive elements that were simultaneously displayed. No attempt was made initially to interpret the intentions or motivational

state of the ant. This is now considered in the light of the experiments. *M. scabrinodis* raises its head and opens its jaws wide when threatening, releasing alarm or attractant pheromone, and prior to an attack (Morgan *et al* 1978). The jaws in the CONFLICT posture were only partly opened and the head was held down. The posture is clearly not as aggressive as a threatening one. Aggression is a stimulus for attack. The partly open jaws are closed when the *Lasius* approaches and examines, presumably to reduce the probability of a more fierce attack. Thus, it is believed that the CONFLICT response possesses an aggressive content that the *Lasius* can detect. Older workers were found to show CONFLICT more than younger ones. These workers are also more aggressive and perform ABDOMEN-CURLING more. The older animals, however, perform additional functions such as recruitment. The poison gland of *M. rubra* increases in size with age and the pheromones emitted from it become increasingly effective (Tricot, 1974). The same may be true of the mandibular gland. The response may, then, not represent opposing tendencies of attack and escape but may be part of more complex and deliberate behaviour. For example, the CONFLICT response may be a compromise between effective pheromone release on the one hand and reducing the aggression of the *Lasius* to a convenient level on the other. Such a situation does occur inside the nest when the *Myrmica* area is invaded by *L. flavus*. In addition, groups of *Myrmica* workers were seen to be attracted to *L. flavus* in the experimental arena and in the shared foraging area of interacting colonies. A pheromone similarly released would facilitate such grouping behaviour and also reduce aggression. The sustainment of the posture for long periods after the *Lasius* had departed from the encounter would favour a functional role rather than the behaviour of an animal with conflicting tendencies. Indeed the latter type of response is usually closely followed by



escape or attack. The animal may attack soon after the response but only in certain circumstances, again suggesting that a strategy is being employed.

The behaviour of *M. scabrinodis* is modified by the actions of the opponent at the individual level. Although the *Myrmica* became passive in pair encounters it did, at times, attempt to approach, threaten and show the CONFLICT response towards the *Lasius*. These activities were seen to stop and the passive postures were assumed again when the *Lasius* attacked it. To substantiate this subjective opinion the CONFLICT response was statistically analysed. The CONFLICT response is terminated by an aggressive *Lasius*. Corpses were fiercely attacked and other responses were performed more and sooner than they were with a live opponent. It is not, therefore, the mere presence of *L. flavus*, i.e. a species or colony contact odour alone, that is the inhibiting influence but an active role played by the ant. The 'active role' may take the form of pheromone emission or tactile aggression.

The *Myrmica* behaved differently to young and old *Lasius*. (Young opponents were less aggressive than older ones - while older animals readily approached and attacked, younger ones remained at a distance performing threat). Consequently, young *Lasius* did not inhibit the CONFLICT response in meetings as much as older ones did. The histograms of Figure 7 illustrate this. The *Myrmica* did behave submissively in encounters with young *Lasius* and the postures were often sustained. Thus, contact aggression (biting, seizing, etc) is not essential for eliciting the submissive response but the response is shown more often and sustained for longer (see Figures 4 and 5 ) if it does occur. The *Myrmica* may respond submissively to the sight of a young, threatening *Lasius* or to the alarm pheromone possibly released from its gaping jaws. The alien pheromones are felt to be the important stimulus (see later).

Some of the quantitative differences in the behaviour of *M. scabrinodis* due to age have been mentioned above. However, age has no major effect on the outcome of pair encounters with *L. flavus* as neither age group examined would attack the opponent.

Starving the *Myrmica* colonies was unsuccessful in initiating the attack response in a 1:1 situation. This is interesting as by increasing the motivation, i.e. the primary feeding drive, the need to fulfil the consummatory act should be great and even weak stimuli should elicit the response. The *Myrmica* will, in certain circumstances, attack and eat *L. flavus*.

The 'drive level hypothesis' proposes that progressively higher levels of drive are needed for the performance of successive responses in the 'chain'. Motivation levels and hunger have been correlated experimentally by Tugendhat (1960) with sticklebacks and Gardner (1964) with salticid spiders. Both authors found that at high levels of hunger the sequence was always carried to completion.

It would seem that at least 2 'sets' of behaviour patterns are occurring together in the *Myrmica* worker. The first one of aggression and predation is inhibited by the second, possibly 'fear' of the aggressive *Lasius*. The evidence of CONFLICT inhibition would support such a theory. The feeding response of sticklebacks is inhibited by high shock levels (Tugendhat, 1960). Holst (1963) has electrically investigated 2 stimulus fields in fish, concerning feeding and escape and describes a range of effects such as: averaging, alternating, cancelling, transforming and masking. One might relate the behaviour of *M. scabrinodis* to some of these processes, such as transformation or masking, but such speculations would need involved experimental verification. Hungry ants normally show a high level of activity which increases on discovering

food (Wallis, 1962b). The rate, duration and latency of locomotion of *M. scabrinodis* are similar in hungry and satiated animals. If hunger does lower the threshold for killing (Lorenz, 1973), it is still not powerful enough in solitary *M. scabrinodis* to override the inhibitory influence stimulated by the aggressive *Lasius*.

The discussion so far has examined the behaviour patterns of the individual in carefully controlled conditions, i.e. the experimental arena. Many of the behaviour patterns that were performed here were also seen when whole colonies interacted. For example, when solitary opponents met in the shared foraging area the *Myrmica* responded submissively and the *Lasius* aggressively. However, the behaviour was found to be variable when colonies interacted and this is believed to be influenced by factors such as numbers and the place of interaction.

A number of *Myrmica* workers are attracted to a *Lasius* and behave passively on meeting it as an individual would in a pair encounter. The aggressive *Lasius* spends a shorter duration attacking each of several opponents than it would a solitary opponent. The *Myrmica* thus enjoy a greater freedom and this results in their becoming closely grouped 'around' the *Lasius* worker. If the *Lasius* is attacked, and the *Myrmica* group often sustain the submissive postures for long periods without doing so, this usually occurs from an ant very close to its side or rear. The close proximity and temporary lack of opponent's aggression seem to be the requirements for an attack. Vowles (1955) has found a similar behaviour in dacetine ants. These ants approach prey very slowly with open jaws and attack when 1 mm away. The labral hairs when touched are thought to stimulate the seizing response. The labral hairs of *M. scabrinodis* (seen in plate 14 page 91 ) may perform

a similar function particularly inside the nest in the absence of light. The behaviour of the pavement ant *Tetramorium caespitum* is similar to *M. scabrinodis* in several ways. Small in size, the ant sometimes behaves passively and will form groups to attack a 'foreign' ant which it could not otherwise subdue. Further, the behaviour of the opponent is thought to influence its aggression (Dobrzanski *et al* 1975). Many authors (e.g. Forel, 1928; Wilson, 1971; Dlussky, 1965) have reported that the aggressiveness of social insects increases as the number of nest-mates grows.

The number of individuals present may increase the probability of an attack but this factor alone is not sufficient for the response to occur in *M. scabrinodis*. Attacks on the *Lasius* were rare in the 'numbers' experiment in the 'arena' but frequent where group behaviour was seen in the shared foraging area.

The 'place of interaction' may influence the aggressiveness of *M. scabrinodis*. The ants will readily attack solitary opponents inside the nest. Similarly, they will rush out and immediately attack a *Lasius* worker near the nest entrance but behave passively if many opponents are there. The ants were seen to be less willing to attack at distances away from the nest. Forel (1928) states that "as a general rule, when an ant strays away from her nest her courage diminishes in a direct ratio to the distance separating her from this nest and her companions". While this may be true in some species, in others it is certainly not the case. For example, many species possess a protected food territory. Stebaev (1971) and Reznitova (1974) have shown that the territory of *Formica pratensis* comprises several zones. The ants are relatively numerous in the area around the nest and sparse in peripheral zones. Nevertheless, battles between *Formica* colonies often begin at frontier incidents where densities were originally low

and may last for days or even weeks (De Bruyn *et al* 1972). Much recruitment takes place and many deaths may result. The territory owners are highly 'motivated' in such sparsely populated areas to fight. Dobrzanski (1975) has observed colonies of *Tetramorium caespitum* and *Lasius brunneus* nesting close together and reports a continual change in dominance relationships between them. The willingness to fight or flight varies but precise conditions are unknown. The actual activity of the nest is believed to have some effect.

Experiments in this study, have shown that the aggressive behaviour of ants may differ at a given place due to the relative colony sizes of the interacting species. When the *Lasius* colony was relatively small the *Myrmica* workers assumed an offensive role.

When the *Lasius* colony was relatively large they assumed an offensive role and the *Myrmica* one of defence. It is interesting that the ABDOMEN-CURLING posture is shown in interactions when the ant is both advancing or retreating! Such species can in some way detect the 'balance of power' and act accordingly. Reznikova (1974) believes that *F. pratensis* detects its territory boundary by sight rather than smell - the ants can learn a location and retain the information overnight so that their return the following day is by visual cues (De Bruyn, 1972). The sight of *M. scabrinodis* and *L. flavus* is inferior to that of *Formica* and communication during interactions is probably by chemical means. Indeed, most interactions between the 2 species will occur inside the nest and thus in the absence of light.

The role of pheromones in the alarm/defence system of ants is well documented for many species (see Wilson, 1971, page 240). The components of the mandibular and Dufour's glands of *M. scabrinodis* have been identified by Morgan *et al* (1978a, 1979), and Cammaerts *et al* (1978) Their findings are very helpful in understanding how the ants may perceive the re-

lative strength of the opposing colony. Both volatile and non volatile substances may be released from Dufour's gland — the former are short lived and cause an increase in the speed of congeners while the latter are longer lasting trail scents. A volatile secretion is produced from the mandibular glands which also may cause alarm. As with all pheromones, the 'active space' depends on the amount of chemical released and the stimulus thresholds of the species. The reaction to a pheromone depends on its intensity. *M. scabrinodis* move slowly over new ground and deposit their scents as they go. The speed increases as more workers lay down their trail pheromone. Ants while most sensitive to pheromones of their own species can detect the odours of other species. Cammaerts (1978) states that *M. scabrinodis* move cautiously in areas marked by other species but that in time the speed increases as they substitute their own markings. In the experiments with a small *L. flavus* colony relatively few *Lasius* venture into the foraging area. The *Myrmica* force is stronger here and this will be reflected in the relative deposition of pheromone. When the *Lasius* colony is large, more of their workers enter the foraging area. Several effects will hinder the release and effectiveness of the *Myrmica* pheromones. Firstly, the *Myrmica* will move around less due to the higher frequency of attacks from the *Lasius*, thus directly reducing trail-laying behaviour. Secondly, the increased amount of *Lasius* secretions may 'mask' those of the *Myrmica* present. The ants can, no doubt, detect a strong or weak alien chemical deposition without reference to their own, and this may be sufficient for a retreat. Morgan (1978) reports that reaction to an alien trail pheromone seems to depend on its intensity. The relative strength of volatile alarm odours may function in a similar way to trail substances in colony assessment. It seems likely that the mechanism used by *M. scabrinodis* to gain information of the strength of the

opposition may also be used by *L. flavus* in a similar way.

It is often said, rather loosely, that interactions between species are influenced by colony activity and 'motivation' of the animals. Both these factors would be reflected in the number of individuals in a given area releasing pheromones.

Tactile cues are thought to play only a minor role in ant communication. Simple associative learning has been demonstrated in ants (Schnierla, 1943). A *Myrmica* worker may respond to the frequency of attacks from a number of *Lasius* and modify its behaviour accordingly. The presence of several opponents will also increase the amount of alien pheromone, contact and volatile, in that area.

The placing by *M. scabrinodis* of their corpses near the *Lasius* nest entrance, and the sustenance of the passive postures by live animals there, is behaviour, which will inform the *Lasius* of their presence and may function to restrict their movement. Bhatkar *et al* 1972, has observed that the fire ant *Solenopsis saevissima* will push dead bodies in front in the form of a barrier in order to gain ground from *Lasius neoniger*.

The *Myrmica* workers not only show a strong attraction to *L. flavus* but also persistently try to enter their nest. Forel (quoted in Donisthorpe, 1927, page 138) and O'Rourke (1950) state that a single worker will enter a *Lasius* nest and return with a corpse. Experiments revealed a mechanism by which successful invasion may be achieved. The extremely slow group advancement of the *Myrmica* performing the passive postures is effective in repelling aggressive opponents even in their own nest - the same behaviour was employed in gaining control of the foraging area. Moreover, the *Myrmica* rarely show threat or attack and thus

the battle is won without fighting or casualties. Many attempts by *M. scabrinodis* to directly enter the alien nest were unsuccessful. In addition, on several occasions in both plaster and soil nests *Myrmica* colonies that had managed to enter were later forcefully evicted by the *Lasius*. Indeed, on such occasions the *Myrmica* showed mass fleeing behaviour.

A normal *Lasius* colony will usually outnumber that of the *Myrmica* by a factor of 10 or even 100. This factor and the persistent and high level of aggression shown by *L. flavus* make it necessary for *M. scabrinodis* to avoid direct confrontation. Experiments show that the ants have evolved a remarkable form of behaviour for doing this. The ants probably enter the alien mound initially by excavation rather than via a *L. flavus* entrance. Indeed, *L. flavus* rarely come above ground and entrances are few and carefully concealed. Once inside the mound, the *Myrmica* must, by some means, remain there against fierce and perhaps continual opposition. The *Myrmica* expend much energy in maintaining their nest identity and many workers are undoubtedly killed in its process. When *L. flavus* succeed in breaking through the soil barrier separating their nests the way *M. scabrinodis* deal with the situations is quite unusual.

Many ant species either attack or 'line up' at a place of danger with gaping jaws. The *M. scabrinodis* quickly assemble (perhaps attracted to the odour of *L. flavus*) at the breach in their nest and by performing and sustaining their ABDOMEN-CURLING posture form a tight wall, which is very effective in physically preventing further *Lasius* from entering. Where the area of interaction is small, for example in a 'tunnel', a single *Myrmica* worker can block the aliens' entry for very long periods. In both cases the blocking behaviour resists fierce attack from the enemy.



Most ant species protect their nest. Nest entrances are usually few in numbers, small in size and guarded. Many species of ant have evolved special forms of workers, usually soldiers or majors, whose function is to block the nest entrances against attack from their enemies. The heads of such "phragmotic" workers are sometimes shield or plug-shaped as in *Pheidole* (Brown, 1967), *Camponotus* (Creighton, 1953; Lee, 1938) and *Paracryptocereus* (Creighton, 1954). *Pheidole multica* has no phragmotic head structures but the same function is performed by a major worker with an enlarged head. The behaviour is usually performed by individuals, at the relatively few nest entrances. However, small groups of workers of *Paracryptocereus* (Kempl, 1952) and *Pheidole multica* (Creighton, 1959) have been seen to cooperate, like *M. scabrinodis*, to seal off a larger nest entrance.\* Firstly, *M. scabrinodis* is monomorphic and has no major workers with specialized phragmotic or enlarged head structures. Instead, the behaviour is determined by age with older, more deeply pigmented workers showing a strong 'preference' for the job. Experiments in pair encounters showed that younger workers will perform the ABDOMEN-CURLING behaviour but to a significantly lesser extent. Secondly, the behaviour is used in interactions inside the nest, rather than at relatively few external nest openings. There are several pieces of evidence which indicate that interactions between the 2 species is an on-going one (persistent *Lasius* aggression, the change in position and ownership of nest cells in naturally-occurring nest mounds and in laboratory colonies, and the thin soil barriers separating the species there) and thus the blocking behaviour is probably commonly employed and by a large number of individuals. Indeed, when *L. flavus* arrives at a location 'unannounced' the nearest *Myrmica* worker at hand will have

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\* The blocking behaviour of *M. scabrinodis* is different from that of previously known examples in several respects.

to extend the 'head of inhospitality' until its nest-mates arrive. Ethal plasticity in worker ants has been discussed by Weir (1958). When a *L. flavus* meets a *Myrmica* worker in a narrow tunnel, plate 6 (page 33 ) shows what the *Lasius* will see, or rather, come up against, a hardened rugose shield of chitin. The antennae are safely retracted and there is little for the *Lasius* to seize. The same is true but to a slightly lesser extent where a group of *Myrmica* cooperate to form a wall. The blocking behaviour combined with rapid building activity enables *M. scabrinodis* to retain its nest identity. Indeed the strongly mudded cells of the ant have been commented on by Brian (1952). The *Myrmica* will not only construct soil barriers but when necessary will fill in nest chambers and tunnels and move away from the sites of interaction. Numbers of *Myrmica* workers were often seemingly stranded in the *Lasius* part of the mound during and after the construction of soil barriers. These workers were attacked fiercely by many *Lasius*. The *Myrmica's* toughness and resistance to a *Lasius* attack was highlighted here. Although some were killed, many survived and it is possible that these may manage to return to their nest.

Communication by stranded ants for example, when buried, is achieved by both stridulation (Markl, 1967) and alarm pheromones (Wilson, 1958). Stridulation and abdomen-tapping on the substratum were observed in *M. scabrinodis* in pair-encounter experiments. There may, in fact, be small 'access points' guarded by a single worker to permit the return of workers.

It was generally felt by myrmecologists in the past that the relationship between *M. scabrinodis* and *L. flavus* was a predator/prey one. The investigations of this study show that the relationship is rather more complex than this and may involve competition. *M. scabrinodis*

will readily and indiscriminately take *Lasius* corpses, alates and pupae back to the nest and eat them. An individual *Myrmica* would often not attack a *Lasius*, although a group of individuals, in some circumstances, would. The experiments show how a single worker can and will enter a *Lasius* nest and remain there for periods against aggressive opposition. The skill and elaborate behaviour permit the predation seen and not the overwhelming aggression that is usually associated with a predatory ant. In fact, the *Lasius* defends its nest and attacks the *Myrmica* in many situations. This is contrary to the statement of Donisthorpe (1927) that the ant is a timid one, even in its own nest, and that it retires deep into the earth when invaded. It is obviously disadvantageous for such a subterranean ant to flee from its nest and feeding territory when attacked. The colonies of *L. flavus* are often large and the workers are concentrated in a relatively small area. Such conditions will favour recruitment and nest defence. Reigner and Wilson (1969) have concluded that the alarm/defence behaviour of the ant *Acanthomyops claviger* is related to its subterranean habits. The ant is strongly attracted to undecane, a chemical released from Dufour's gland at time of alarm. The same chemical and in lower concentrations causes greater excitement without such attraction in the above-ground forager *L. alienus*. A similar chemical investigation of *L. flavus* related to the behaviour in its nest would be interesting.

Although *M. scabrinodis* kill and eat *L. flavus* the extent of the predation is questionable. Long periods were often observed where few, if any, *Lasius* were taken. The *Myrmica* were hungry, yet their aggressiveness at the nest entrance was inhibited by the opponents as in pair encounter experiments. The large build up of yellow head capsules on the *Myrmica* refuse pile has been regarded as evidence of predation in

the past. However, these may be the result of nest interactions.

Nest interactions may be due to competition.

Interspecific competition has been examined by several authors. (Park, 1954; Brian, 1956a; Birch, 1957; Hardin, 1960; Milne, 1961). Pontin (1961) states that "interspecific competition is occurring if lower densities of the competitors are found than would be the case if each were present alone". When Pontin (1969) removed colonies of *M. scabrinodis* from the nest mounds of *L. flavus* the latter showed an increase in alate production. The author has seen progressive decline in *Lasius* worker numbers over several years where *M. scabrinodis* occupy the same mound. Competition in ants is usually for 2 basic resources - nest site and food. Both these resources are considered by Brian (1965, pages 66-77).

The number and availability of nest sites is a common and primary control of colony density throughout the social insects. Many ant species are restricted to dead wood in tropical forests (Wilson, 1959b) and fierce intraspecific competition takes place in termites where trees are in demand (Greaves, 1962). Colony density with respect to nest site availability has been reported in *Myrmica* by Gosswald (1951 and Brian (1956b). The destruction of small colonies and occupation of their nests by larger ones is common (see Forel, 1928). Both *Myrmica* (Brian, 1952a) and *Formica* (Scherba, 1964) have been reported to take nests of other species of their genus.

The habitat requirements of *M. scabrinodis* and *L. flavus* are very similar (see Introduction). Both species prefer dry, warm situations where the nest temperature favours development of their brood. The vegetation of an area increases when grazing by mammals is reduced or absent. The *L. flavus* are able to construct large and elaborate mounds to help compensate for this. Many species, such as *M. scabrinodis* and *Formica lemari*, etc., are poor builders and are thus normally restricted

to bare surfaces. It is believed that the favourable nest site of the *Lasius* mound is a major reason for the invasion and co-occupancy frequently encountered and for the many aggressive interactions and deaths to both species that result. When a small stone is present near *Lasius* colonies it is often occupied by a *M. scabrinodis* nest. Brian (1952a) reports that *M. scabrinodis* will compete fiercely with *M. ruginodis* for a favourable site beneath a stone and may capture nest territory in 3 ways: firstly, by direct seizure which causes fleeing in the opponents; secondly, by its ability to re-enter the nest quickly following a period of poor climatic conditions; and thirdly, by gradual encroachment. *M. ruginodis* were killed during interactions and the corpses eaten. Many species will consume the victims of battles. Nest capture by *M. scabrinodis* from *L. flavus* is also by a gradual encroachment. The experiments show precisely how this can be achieved against aggressive opposition. The author has often found *M. scabrinodis* nesting in the S. - S.W. part of the mound, which is presumably the most favourable position of the 'incubator'. Where a stone is placed on top of the mound, *M. scabrinodis* often occupies a large proportion of it. Such a reduction in part of the most favourable area of the nest may be a contributory factor for the reduced alate population recorded by Pontin (1969). Competition may thus be occurring. The term 'competition' is employed for, in the absence of one species the other would occupy more of the favourable nest area. However, the *Myrmica* population may decrease in the absence of the *Lasius* colony (due to an overriding food factor or an inability to maintain the elaborate nest structure of the *Lasius*). Odum (1953, page 165) states that there are 8 ways that 2 species may interact. If, as proposed, *M. scabrinodis* benefits from the *Lasius* nest site, and the *Lasius* suffers from its presence then the +/- relationship, as classified by Odum, is either parasitism or predation.

Unless the term 'nest-site predation' is employed a new term is necessary.

It is believed that the 2 species may also be competing for food. *M. scabrinodis* forages both above and below ground. Independent colonies tend aphids (Pickles, 1936) and the ants will construct earthen cells on plants to cover them. The feeding territory of *L. flavus* is effectively 2 dimensional (Pontin, 1961). Sudd (1970) has investigated the tunnel shape of *M. scabrinodis* and finds that these spread and branch beneath the surface relatively more than other species examined. *M. scabrinodis* are found at distances away from their concentrated nest area within the *Lasius* feeding territory. A *Myrmica* will almost certainly 'milk' or eat aphids that it encounters there. In fact root aphids may be a far more attractive food item than *Lasius* workers. The rate of feeding in animals is a function of the intensity of the eliciting stimulus. The size, palatability, abundance and ease of access of the food can all influence the feeding response. The nutritive value of aphids is probably greater than that of *Lasius* workers, they are often very abundant (Pontin, 1978) and they are certainly less aggressive and less dangerous than a potential *Lasius* prey.

The 'invasion' behaviour and building activity of *M. scabrinodis* was seen to be effective in capturing nest areas belonging to the *Lasius*. It would seem feasible that the behaviour may also be employed to capture underground chambers where aphids occur. Experimental investigation of aphid and nest site competition, where the effect on the populations of each species is examined, would seem a worthwhile study.

It is proposed that the relationship between *M. scabrinodis* and *L. flavus* is a complex one, possibly involving the predation of *Lasius* workers and brood, and competition for nest site and root aphids.

*M. scabrinodis* and *L. flavus* form a 'compound nest' as their workers are hostile to one another and their broods are kept separate. Many examples of species living in compound nests have been recorded (Wheeler, 1901, 1903, 1904, 1921; Forel, 1928; Stumper, 1949; Wilson, 1971). Terms such as plesiobiosis, lestobiosis and cleptobiosis have been applied to various relationships that occur in compound nests but none of these fit the example found here. The coining of a new term would seem pointless as, no doubt, many more associations will be discovered each different from the last and requiring a new term.

CHAPTER 4

INDIVIDUAL INTERACTIONS BETWEEN

*M. SCABRINODIS* AND 5 DIFFERENT ANT SPECIES.



## 1. Introduction and Method.

It has been stated earlier than an ant can detect the pheromones of an alien and that its behaviour may vary according to the intensity of the stimulus. Many pheromone studies have been done in both *Myrmica* (Maschwitz, 1966; Crew and Blum, 1970; Cammaerts - Tricot, 1972, 1974a, b, c, d; 1977, 1978; Morgan *et al* 1977, 1978, 1979) and *Lasius* (Bernardi *et al.*, 1967; Blum, 1968; Reignier and Wilson, 1968, 1969; Bergstrom and Lofquist, 1970). However, surprisingly little is known of the ants' ability to distinguish different chemicals and of their reaction to them. Competition requires intra and interspecific communication, which in ants is almost certainly transmitted by chemical means.

The following experiments investigate the behavioural responses of *M. scabrinodis* to 4 different ant species, in addition to *L. flavus*, that commonly occur in the same habitat. The behaviour of individual *M. scabrinodis* workers was recorded in pair-encounter experiments with *M. scabrinodis* (from an alien colony), *M. rubra*, *L. niger* and *L. umbratus*. The 'General Method' was closely followed for each of the 4 experiments. The behaviour of *M. scabrinodis* towards *L. flavus* is given in (page 30).

## 2. Results.

### 2.1. Interactions.

#### 2.1.1. *M. scabrinodis* vs. *M. scabrinodis* (from an alien colony).

Mean scores for the acts shown by *M. scabrinodis* in encounters with an opponent of the same species, but from a different colony, are given in Table 27. None of the acts showed a significant temporal patterning effect (see Appendix, Table 12). One, and sometimes both, ants of the pair seized the opponent at the first meeting. This occurred in every replicate trial. The ants then remained in contact throughout

TABLE 27. Mean Scores for the responses shown by individuals of *M. scabrinodis* in pair encounters with alien *M. scabrinodis* (n = 10).

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	0.9	n.a.
AVOID	0.0	n.a.
MEET	7.3	1748.4
THREAT	4.8	138.2
CONFLICT	1.2	38.2
LUNGE	1.2	n.a.
BITE	0.9	n.a.
SEIZE	10.5	939.8
DRAG	6.2	274.0
STING	3.3	95.4
CHASE	0.0	n.a.
FLEE	0.0	n.a.
GROOM	1.3	8.8
LOCOMOTION	3.7	39.2
STILL	2.3	244.8
ABDOMEN CURLING	0.3	.17.6

the experiment. Scores for seizing duration were, consequently, very high. The striking feature of combats was that they did not appear to be fierce - little struggling was seen, locomotion was not rapid and scores for grooming were low. Indeed, both ants remained motionless for long periods when seizing or when being seized. The ants were often 'face-to-face', each holding the other's antenna or jaw. Antenna/antenna contact was frequent and rapid in otherwise motionless opponents. Other parts of the body grasped for long periods include the neck and petiole. Much dragging occurred but this was also not considered to be severe as fierce pulling movements and active struggling were rarely seen. The animal being 'dragged' often walked in unison with its captor. The stinging behaviour often resembled the ABDOMEN-CURLING posture. The abdomen was often curled slowly and sustained for a while. This is in contrast to the short rapid stinging movements seen in fierce combats between *M. scabrinodis* and *M. rubra*. The abdomen was also employed in a rapid tapping motion of its tip on the substratum. This was a regular occurrence and was performed by most ants. All ants were alive after 24 hours. Five pairs were still involved in seizing behaviour while the other 5 pairs were not in contact with each other. The acts AVOID, CHASE and FLEE were never shown. This may be explained by the ants fighting at the first meeting and remaining in contact for the rest of the encounter. Low scores for APPROACH, GROOM, and LOCOMOTION may also be related to this factor. Few "INTER-MEET" periods occurred and therefore further analysis of CONFLICT behaviour and of the sustainment of STILL and ABDOMEN-CURLING postures was not possible.

#### 2.1.2. *M. scabrinodis* vs. *M. rubra*.

On meeting its opponent *M. rubra* exhibited a range of differing responses but in most interactions both species behaved aggressively

TABLE 28. Mean Scores for the responses shown by individuals of *M. scabrinodis* in pair encounters with *M. rubra*.  
(n = 10).

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	3.6	n.a.
AVOID	1.2	n.a.
MEET	18.8	1468.2
THREAT	13.3	95.0
CONFLICT	1.2	115.6
LUNGE	3.8	n.a.
BITE	6.0	n.a.
SEIZE	20.7	631.8
DRAG	17.9	434.0
STING	4.1	39.6
CHASE	5.3	n.a.
FLEE	0.2	n.a.
GROOM	6.1	56.8
LOCOMOTION	11.6	130.4
STILL	0.8	21.6
ABDOMEN CURLING	0.4	21.4

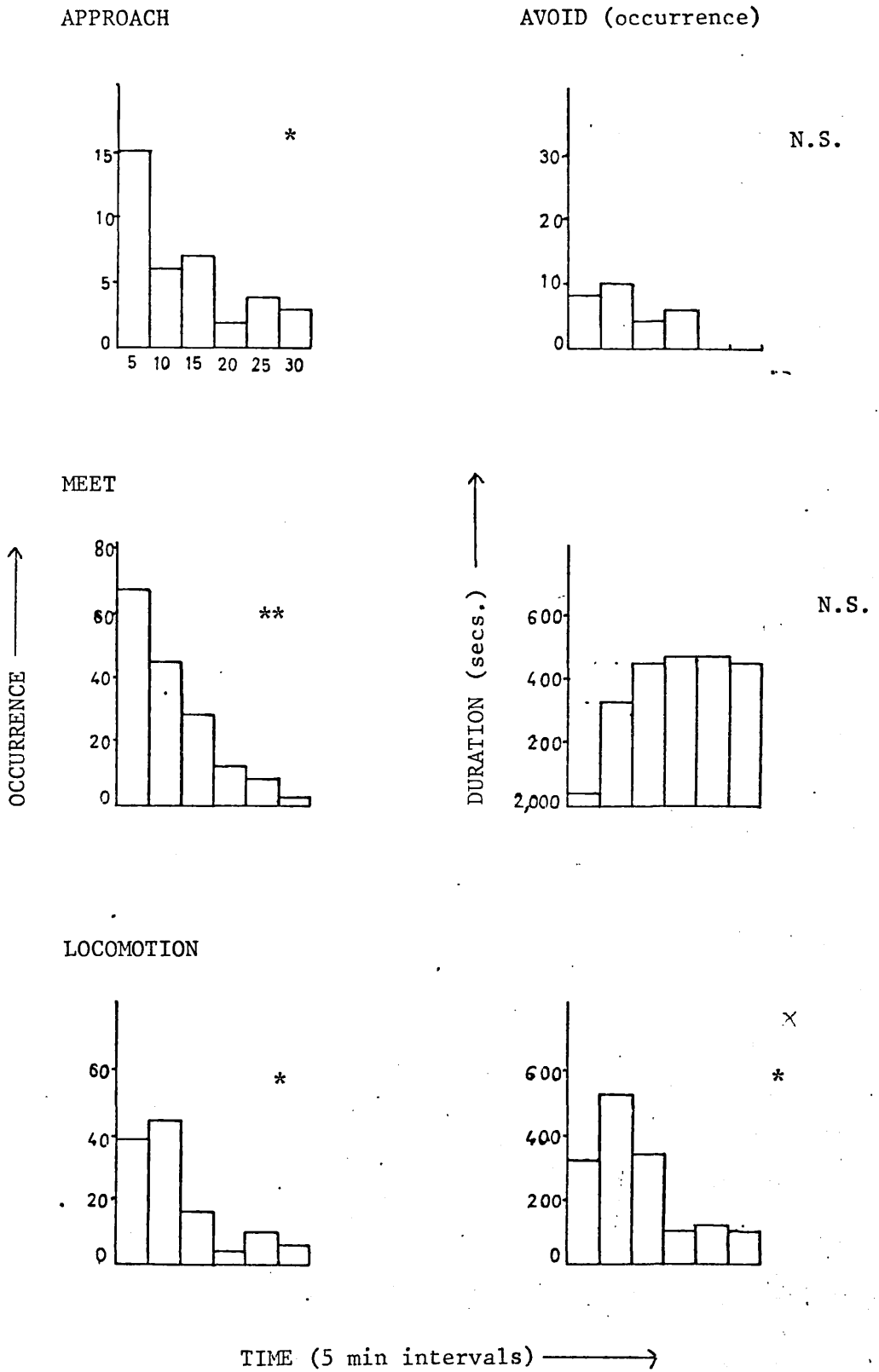


FIGURE 18(a) Temporal patterning of responses shown by *M. scabrinodis* in 30 minute pair encounters with *M. rubra* (see KEY, page 50 ).

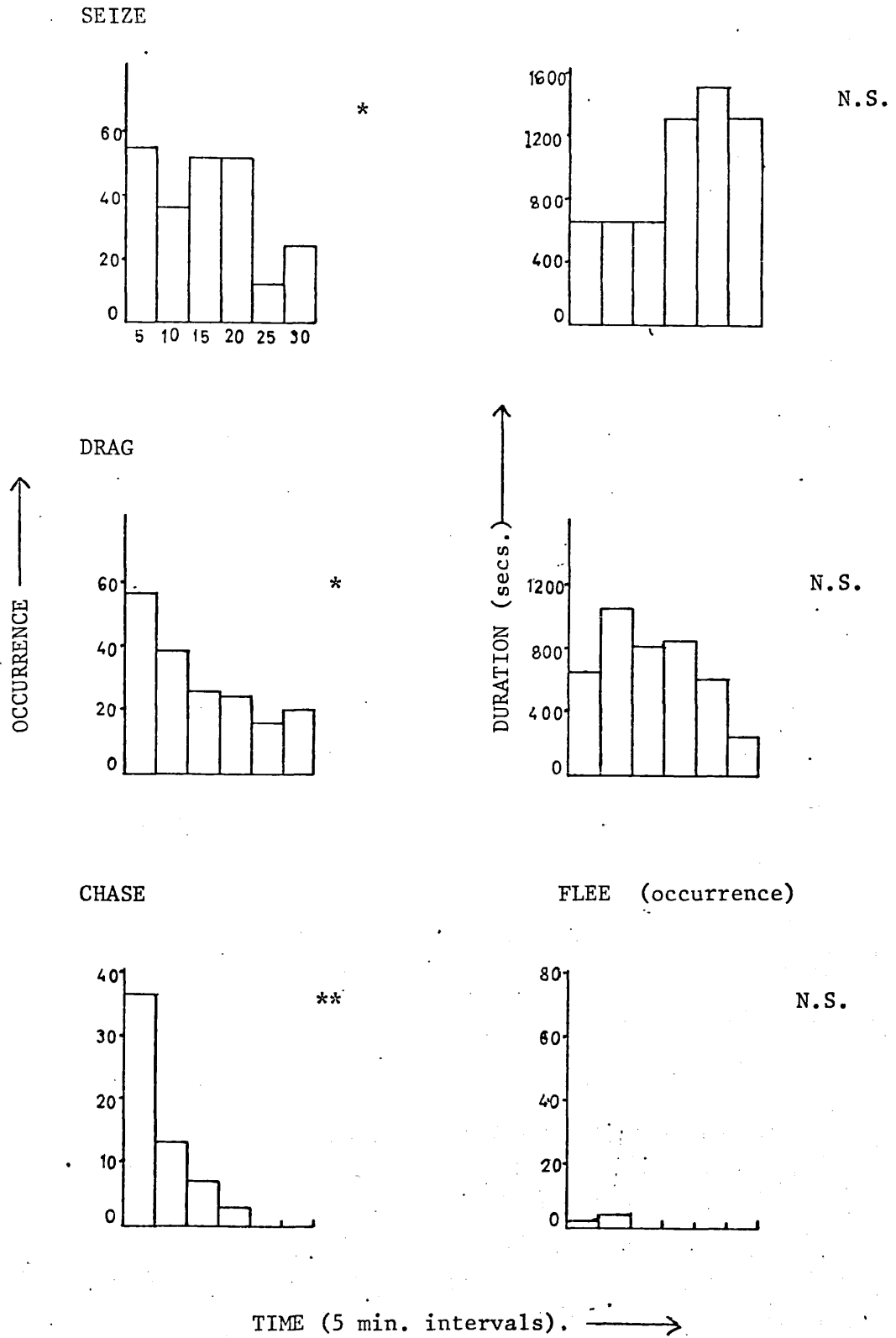


FIGURE 18(b) Temporal patterning responses shown by *M. scabrinodis* in 30 minute pair encounters with *M. rubra*. (see KEY, page 50 )

and fighting occurred. Mean scores for the acts shown by *M. scabrinodis* in encounters with *M. rubra* are given in Table 28. An analysis of the temporal patterning of all responses is given in the appendix (Table 11). Behaviours that changed significantly with time are illustrated in Figure 18. *M. scabrinodis* often approached and chased the opponent. These two acts were shown significantly more in the initial minutes of the encounter (see Figure 18a and f). Fleeing was rarely seen. In meetings THREAT and some CONFLICT were performed. Occasionally, both opponents performed THREAT at each other simultaneously and remained in this posture for a time. No CONFLICT was performed in the INTER-MEET period (see Figure 22 Page 130). When fighting occurred it was often fierce and lasted for long periods. Consequently, meetings were relatively few but of long duration. More meetings occurred in the initial periods of the encounter (see Figure 18b). Some lunging and biting was observed. The opponent was seized and dragged a great deal. Seizing and dragging were shown more often in the earlier periods of the encounter (see Figures 18d and e). The duration of these two acts did not follow a similar pattern. Indeed, the opposite effect may be the case. Abdomens were employed in stinging motions by both species during combat. After 24 hours, 8 *M. scabrinodis* and 2 *M. rubra* were found dead. When *M. scabrinodis* groomed itself it did so for relatively long periods. An amount of locomotion was performed and this occurred more and for longer in the initial periods of the encounter (see Figure 18c). The STILL and ABDOMEN-CURLING acts were done very little and therefore the sustainment of these postures was not analysed.

#### 2.1.3. *M. scabrinodis* vs. *L. niger*.

*L. niger* showed several different responses on meeting its opponent. Avoidance and fleeing were shown by a proportion of ants, particularly in initial meetings. Sometimes the enemy was approached and attacked.

TABLE 29. Mean Scores for the responses shown by individuals of *M. scabrinodis* in pair encounters with *L. niger*. (n = 10)

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	7.6	n.a.
AVOID	1.1	n.a.
MEET	31.5	628.8
THREAT	14.5	291.8
CONFLICT	10.3	270.2
LUNGE	1.7	n.a.
BITE	0.6	n.a.
SEIZE	2.5	56.2
DRAG	2.0	50.6
STING	1.9	17.6
CHASE	2.3	n.a.
FLEE	0.1	n.a.
GROOM	1.5	20.2
LOCOMOTION	20.4	311.4
STILL	7.8	160.4
ABDOMEN CURLING	9.8	263.0



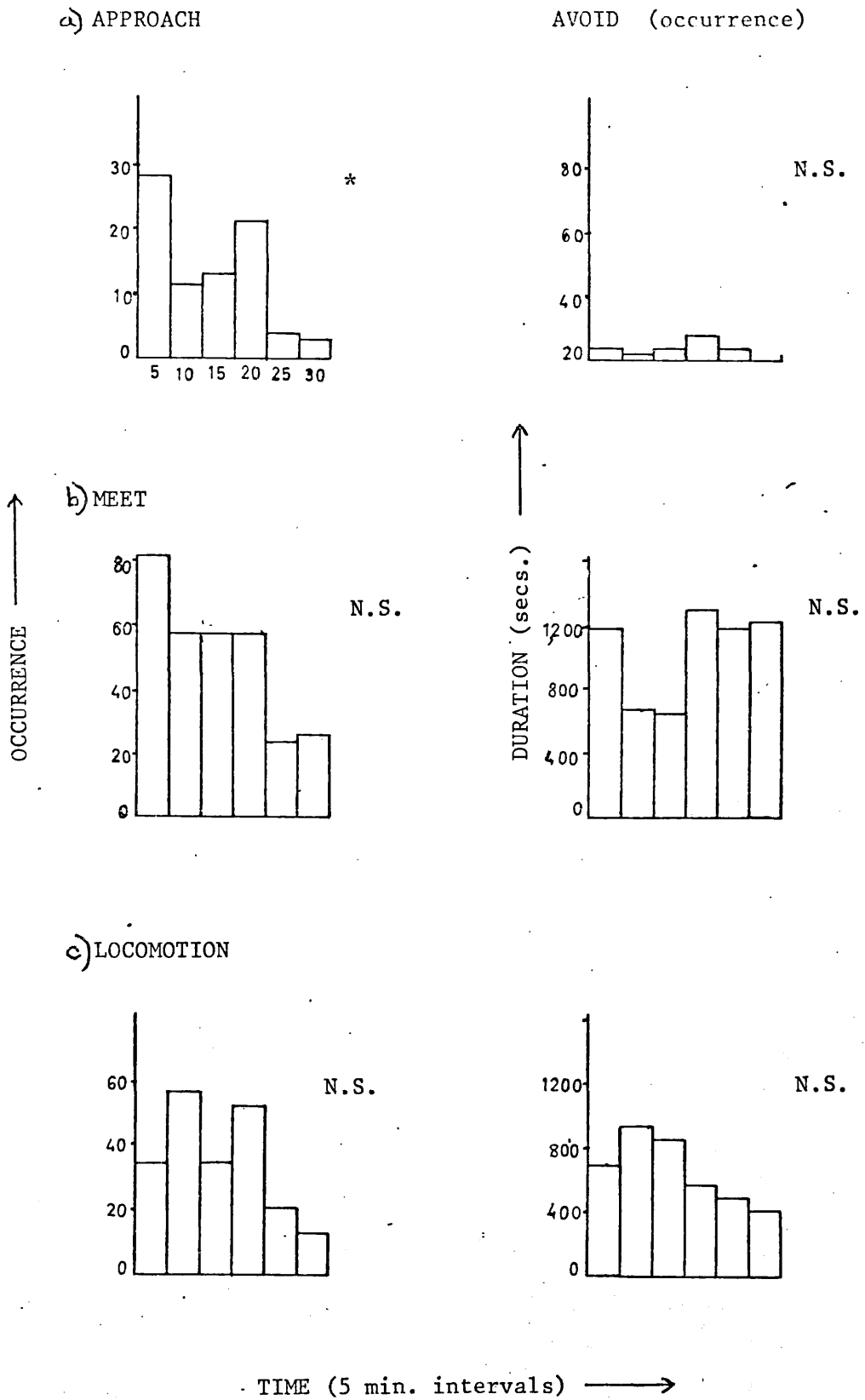
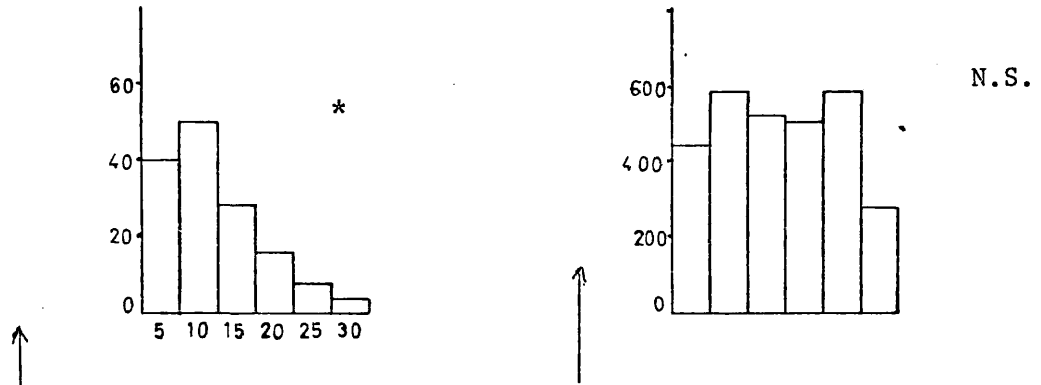


FIGURE 19(a) Temporal patterning of responses shown by *M. scabrinodis* in 30 minute pair encounters with *L. niger*. (see KEY, page 50 ).

d) THREAT



e) CONFLICT

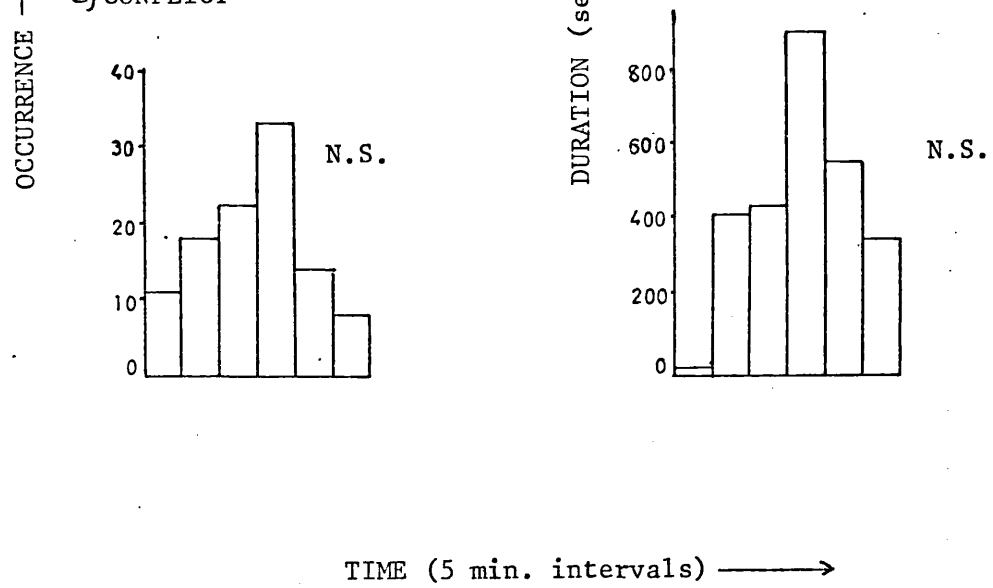


FIGURE 19(b) Temporal patterning of responses shown by *M. scabrinodis* in 30 minute pair encounters with *L. niger* (see KEY, page 50 ).

TABLE 30. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. niger*

COMPARED WITH

*M. scabrinodis* vs. *L. niger* (Dead)

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	27.0	N.S.	-	6.5	***	1	n.a.	-	-
AVOID	19.5	*	2	22.0	*	2	n.a.	-	-
MEET	n.a.	-	-	7.5	***	1	29.0	N.S.	-
THREAT	30.5	N.S.	-	9.0	***	1	10.0	***	1
CONFLICT	10.0	***	1	10.0	***	1	10.0	***	1
LUNGE	38.5	N.S.	-	40.0	N.S.	-	n.a.	-	-
BITE	45.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
SEIZE	47.0	N.S.	-	48.0	N.S.	-	50.0	N.S.	-
DRAG	49.5	N.S.	-	46.5	N.S.	-	48.5	N.S.	-
STING	45.0	N.S.	-	46.0	N.S.	-	46.0	N.S.	-
CHASE	n.a.	-	-	n.a.	-	-	n.a.	-	-
FLEE	45.0	N.S.	-	45.0	N.S.	-	n.a.	-	-
GROOM	27.0	N.S.	-	32.5	N.S.	-	37.5	N.S.	-
LOCOMOTION	24.5	N.S.	-	45.5	N.S.	-	23.0	*	2
STILL	31.5	N.S.	-	41.5	N.S.	-	35.5	N.S.	-
ABDOMEN CURLING	15.5	**	1	20.0	*	1	20.0	**	1

Some *Lasius* which avoided initially attacked in subsequent meetings. A high level of activity was displayed in interactions. The speed of the *Lasius* was judged to be much faster than that of the *Myrmica*.

The behaviour of the *Myrmica* was variable on meeting its opponent. Mean scores for the acts shown by *M. scabrinodis* in encounters with *L. niger* are given in Table 29. Acts that changed significantly with time are illustrated in Figure 19. An analysis of the temporal patterning of all responses is given in the Appendix (Table 10). The *Lasius* was usually approached rather than avoided. Chasing often occurred and fleeing was rarely seen. Much CONFLICT was shown in both the presence and absence of the opponent. (see Figure 22, page 130). A great deal of THREAT was shown in confrontations. Both APPROACH and THREAT were performed more often in the first minutes of the encounter (Figure 18a and d). The same effect is not true of CONFLICT (Figure 18e). Some *Myrmica* attacked the opponents and, here, fighting occurred. Such fights were occasionally fierce. Gasters were employed in combat, by both species, in the quick flexing movement typical of stinging behaviour. 3 *Myrmica* and 4 *Lasius* were dead after 24 hours. The STILL and ABDOMEN-CURLING postures were performed in some interactions. The sustainment of these postures in the INTER-MEET periods is shown in Figure 21.

The behaviour of *M. scabrinodis* towards live and dead workers of *L. niger* is compared in Table 30. The ant behaves differently towards live and dead animals in several respects. Scores for APPROACH, THREAT, CONFLICT and ABDOMEN-CURLING are higher with the live opponents. Scores for AVOID and LOCOMOTION are higher in encounters with dead animals. The aggressive acts were displayed to both experimental groups and no significant differences are found between them.

#### 2.1.4. *M. scabrinodis* vs. *L. umbratus*.

The behaviour of *L. umbratus* was very similar in most interactions.

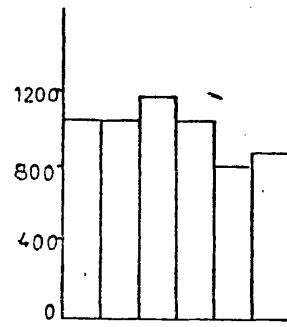
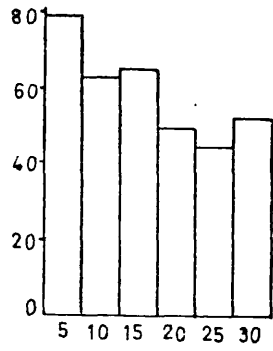
Typically, the *Lasius* approached, examined and attacked its opponent. The aggression consisted of biting, seizing and pulling actions. Antennal activity was vigorous. The abdomen was not usually employed in attacks.

*M. scabrinodis* behaved in several ways on meeting its opponent. The mean scores for the act shown by *M. scabrinodis* in encounters with *L. umbratus* are displayed in Table 31. Behaviours that changed significantly with time are shown in Figure 20. An analysis of the temporal patterning of all responses is given in the Appendix (Table 9). The STILL and ABDOMEN-CURLING postures were often performed and fighting did not occur in the vast majority of interactions. More time was spent by the *Myrmica* displaying the 'passive' acts than any others. The STILL act was shown for relatively longer early in the encounters (see Figure 20c). Both 'passive' acts were sometimes sustained after the *Lasius* had departed - at other times, locomotion began immediately. Figure 21 (page 128) shows the frequency and duration of these sustained behaviours at the end of a meeting. *M. scabrinodis* often approached and rarely avoided its opponent. THREAT was shown in interactions. CONFLICT was shown in both the presence and absence of the enemy (see Figure 22, page 129). The CONFLICT posture sustained in the INTER-MEET period was sometimes relinquished when the opponent approached and attacked it at the next meeting - at other times, CONFLICT behaviour was not terminated (see Figure 23). The *Myrmica* attacked the *Lasius* on only a few occasions but here combats were rigorous and fierce. *L. umbratus* used its abdomen in fierce combats and fleeing behaviour by the *Myrmica* was seen to result. The *Myrmica* showed signs of injury after some fights, for example by the sporadic and feeble movement of limbs. Long bouts of self-grooming also accompanied fighting. Two *Myrmica* and 6 *Lasius* were found dead after 24 hours.

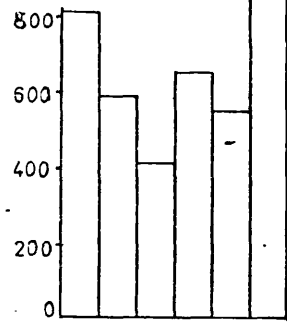
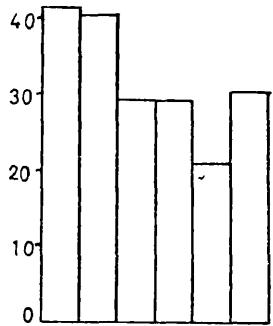
TABLE 31. Mean Scores for the responses shown by individuals of *M. scabrinodis* in pair encounters with *L. umbratus*. (n = 10).

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	9.7	n.a.
AVOID	0.2	n.a.
MEET	35.5	591.4
THREAT	3.4	26.6
CONFLICT	9.0	146.2
LUNGE	0.5	n.a.
BITE	0.5	n.a.
SEIZE	1.0	12.8
DRAG	0.2	1.4
STING	0.3	2.0
CHASE	0.2	n.a.
FLEE	2.1	n.a.
GROOM	3.4	43.0
LOCOMOTION	19.1	381.0
STILL	20.0	395.0
ABDOMEN CURLING	17.7	568.8

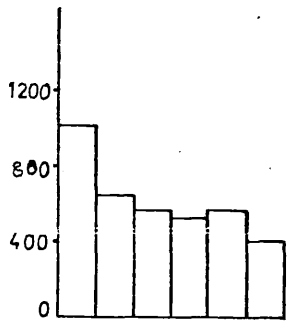
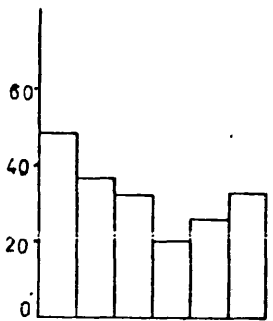
a) MEET



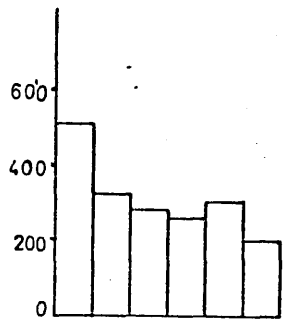
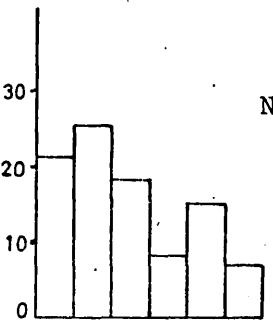
b) LOCOMOTION



c) STILL



d) CONFLICT



TIME (5 min. intervals) →

FIGURE 20 Temporal patterning of responses shown by *M. scabrinodis* in 30 minute pair encounters with *L. umbratus* (see KEY, page 50 )

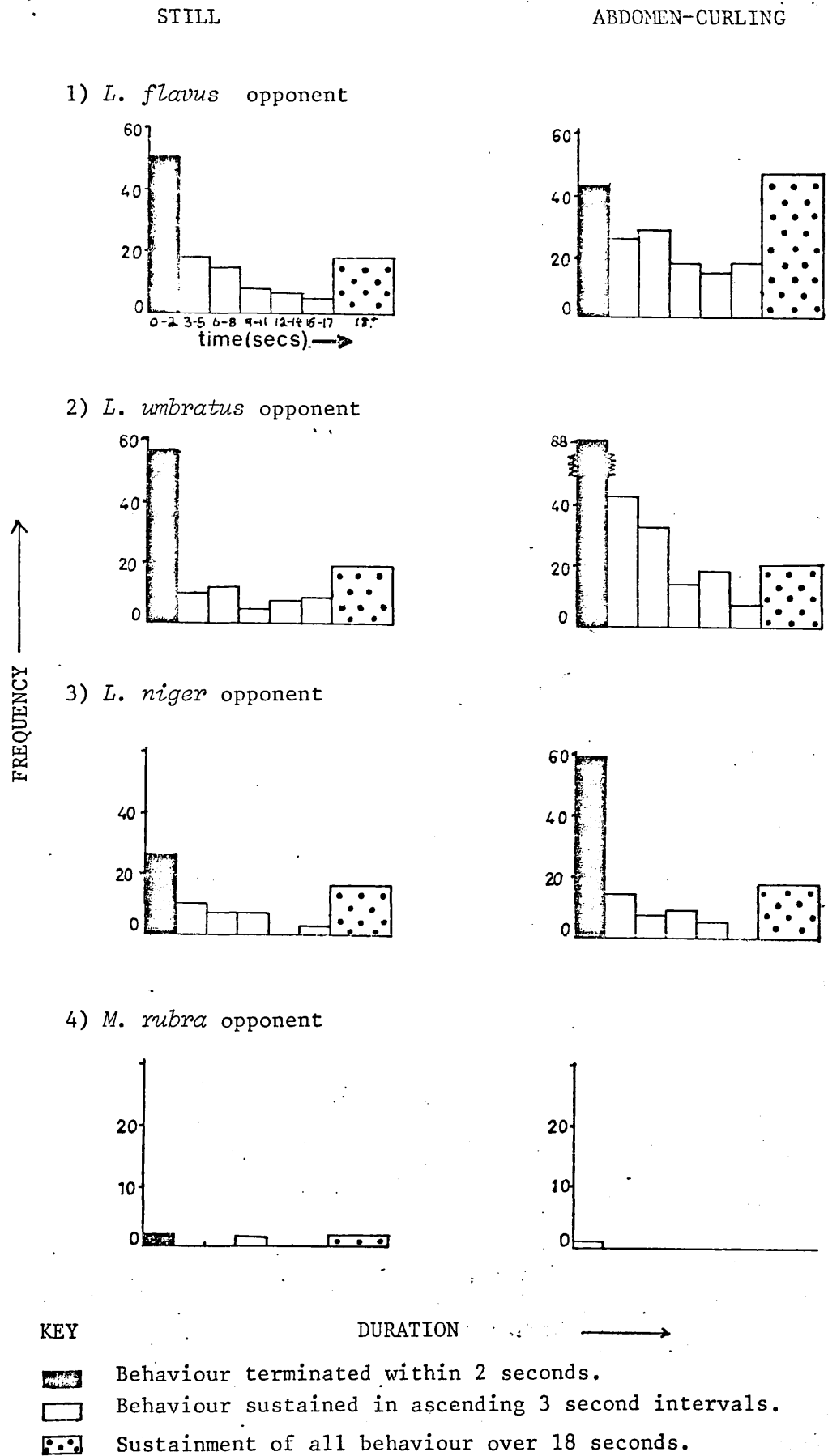
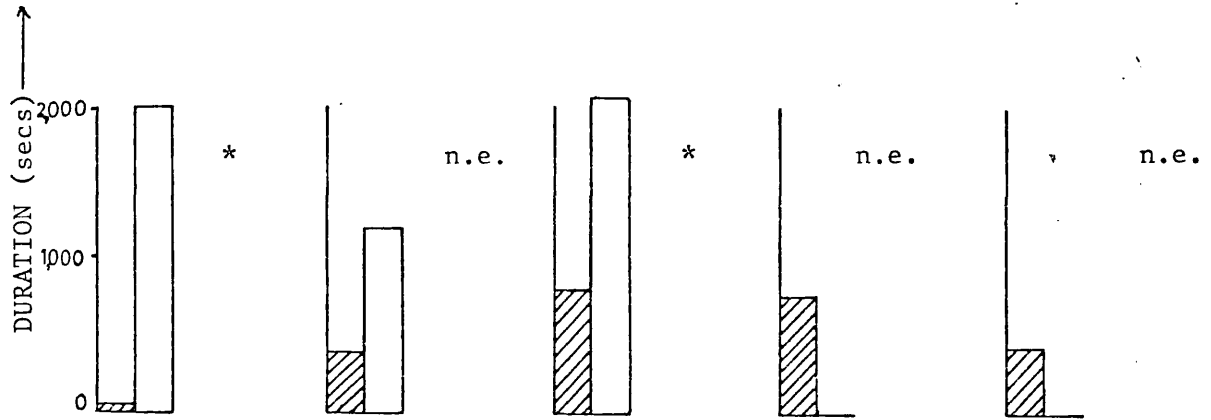


FIGURE 21. Sustainment of the STILL and ABDOMEN-CURLING responses by *M. scabrinodis* after meeting in pair encounter experiments with 4 different ant species.



1) *L. flavus*    2) *L. umbratus*    3) *L. niger*    4) *M. rubra*    5) *M. scabrinodis*



KEY



MEET period



INTER-MEET period

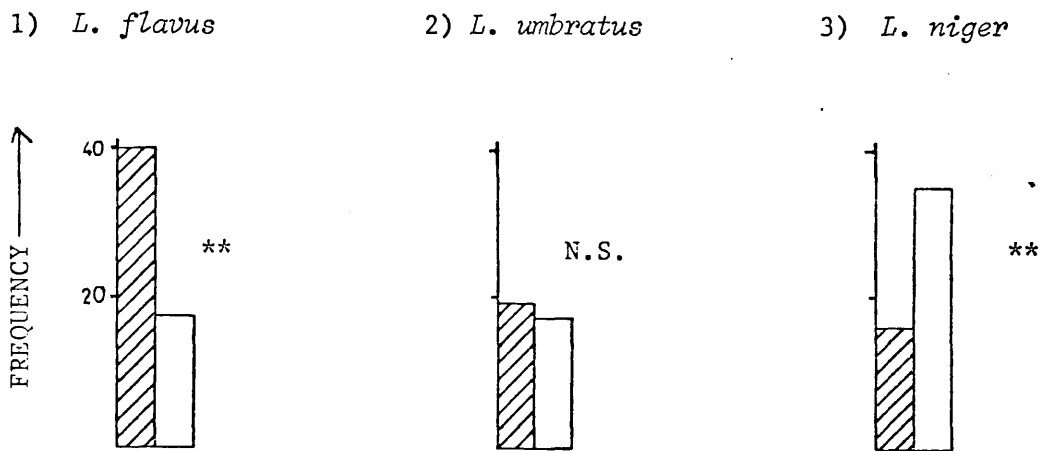
\*

$p < 0.05$

n.e.

not examined - insufficient data.

FIGURE 22. Comparison of the CONFLICT response performed in the MEET and INTER-MEET periods by *M. scabrinodis* in pair encounters with 5 different ant species.



- 4) *M. rubra* - behaviour was not sustained in the absence of *M. rubra*  
5) *M. scabrinodis* - behaviour was not sustained in the absence of *M. scabrinodis*.

KEY



Behaviour terminated immediately.



Behaviour sustained.

\*\*  $p < 0.01$

N.S. Not significant.

FIGURE 23. Termination/sustainment of the CONFLICT response shown by *M. scabrinodis* when confronted by the opponent in 5 types of pair encounters.

## 2.2. Comparison of the Interactions.

### 2.2.1. Aggressive behaviour of *M. scabrinodis* to 3 *Lasius* species.

The behaviour of *M. scabrinodis* is compared in encounters with *L. flavus*, *L. umbratus* and *L. niger* in Tables 32-34. The behaviour of the ant was similar to all 3 *Lasius* in many respects. Often fighting did not occur in interactions with each of the species. No significant differences are present in the aggressive acts LUNGE, BITE, SEIZE, DRAG and STING for all 3 measures. Also no differences appear in the acts LOCOMOTION and GROOM.

*M. scabrinodis* did behave differently to the 3 opponents in some respects. Interactions were judged to be the most fierce with *L. niger*. This ant is threatened sooner, more often and for longer than are the other two species. *L. niger* is chased sooner and more often than is *L. flavus*. CONFLICT is performed for longer periods with respect to the former. ABDOMEN-CURLING is shown for much less time with *L. niger* than with both other *Lasius*. STILL is shown less often, for less time and later on than with *L. flavus*.

Encounters were observed to be the least aggressive with *L. flavus*. Typically, at each meeting a passive posture was adopted: no fighting ensued. While some deaths followed from interactions with both *L. umbratus* and *L. niger*, none occurred with *L. flavus*. In the comparisons in Tables 32 and 33, ABDOMEN-CURLING is done for longer and LOCOMOTION for less time with *L. flavus* than with both other *Lasius*. It should be noted that the *Myrmica* fled from *L. umbratus* sooner and more often than from the other 2 species.

### 2.2.2. Intraspecific and Intrageneric Aggression.

The behaviour of *M. scabrinodis* in encounters with alien *M. scabrinodis* and with *M. rubra* is compared in Table 35. Con-generic fighting was more intense than con-specific fighting. *M. rubra* was chased, seized

TABLE 32. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH *M. scabrinodis* vs. *L. umbratus*  
 (test animal) (opponent) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	30.5	N.S.	-	27.5	N.S.	-	n.a.	-	-
AVOID	33.0	N.S.	-	22.5	*	1	n.a.	-	-
MEET	n.a.	-	-	22.0	*	2	37.5	N.S.	-
THREAT	37.0	N.S.	-	31.5	N.S.	-	31.0	N.S.	-
CONFLICT	38.5	N.S.	-	46.5	N.S.	-	48.0	N.S.	-
LUNGE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
BITE	35.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
SEIZE	35.0	N.S.	-	35.0	N.S.	-	35.0	N.S.	-
DRAG	40.0	N.S.	-	40.0	N.S.	-	40.0	N.S.	-
STING	40.0	N.S.	-	40.0	N.S.	-	40.0	N.S.	-
CHASE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
FLEE	15.0	**	2	15.0	**	2	n.a.	-	-
GROOM	41.0	N.S.	-	42.0	N.S.	-	38.0	N.S.	-
LOCOMOTION	21.0	*	2	21.5	*	2	20.0	*	2
STILL	34.5	N.S.	-	7.5	***	2	24.0	N.S.	-
ABDOMEN CURLING	33.0	N.S.	-	31.5	N.S.	-	7.0	***	1

TABLE 33. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. niger* COMPARED WITH *M. scabrinodis* vs. *L. flavus*  
 (test animal) (opponent) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	29.0	N.S.	-	30.5	N.S.	-	n.a.	-	-
AVOID	46.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	42.0	N.S.	-	38.0	N.S.	-
THREAT	9.0	***	1	4.0	***	1	4.5	***	1
CONFLICT	39.0	N.S.	-	23.5	N.S.	-	22.0	*	1
LUNGE	30.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
BITE	35.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
SEIZE	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
DRAG	35.0	N.S.	-	35.0	N.S.	-	35.0	N.S.	-
STING	35.0	N.S.	-	35.0	N.S.	-	35.0	N.S.	-
CHASE	20.0	*	1	20.0	*	1	n.a.	-	-
FLEE	45.0	N.S.	-	45.0	N.S.	-	n.a.	-	-
GROOM	46.0	N.S.	-	45.5	N.S.	-	41.5	N.S.	-
LOCOMOTION	41.0	N.S.	-	23.0	*	1	24.0	N.S.	-
STILL	27.5	N.S.	-	34.5	N.S.	-	42.0	N.S.	-
ABDOMEN CURLING	18.0	**	2	37.5	N.S.	-	1.0	***	2

TABLE 34. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. niger* COMPARED WITH *M. scabrinodis* vs. *L. umbratus*  
 (test animal) (opponent) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	45.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
AVOID	34.0	N.S.	-	31.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	34.0	N.S.	-	49.0	N.S.	-
THREAT	17.0	**	1	11.5	**	1	16.0	**	1
CONFLICT	46.0	N.S.	-	28.5	N.S.	-	25.5	N.S.	-
LUNGE	39.0	N.S.	-	35.5	N.S.	-	n.a.	-	-
BITE	49.0	N.S.	-	49.0	N.S.	-	n.a.	-	-
SEIZE	42.0	N.S.	-	39.5	N.S.	-	38.0	N.S.	-
DRAG	44.0	N.S.	-	42.0	N.S.	-	38.5	N.S.	-
STING	46.0	N.S.	-	43.5	N.S.	-	44.0	N.S.	-
CHASE	34.0	N.S.	-	24.0	N.S.	-	n.a.	-	-
FLEE	15.0	**	2	15.0	**	2	n.a.	-	-
GROOM	47.0	N.S.	-	48.5	N.S.	-	46.5	N.S.	-
LOCOMOTION	35.5	N.S.	-	46.5	N.S.	-	41.5	N.S.	-
STILL	7.5	***	2	15.0	**	2	19.0	**	2
ABDOMEN CURLING	34.0	N.S.	-	28.0	N.S.	-	21.5	*	2

TABLE 35. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *M. scabrinodis*

COMPARED WITH *M. scabrinodis* vs. *M. rubra*.

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	46.0	N.S.	-	20.0	*	2	n.a.	-	-
AVOID	40.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	4.5	***	2	7.0	***	1
THREAT	48.0	N.S.	-	34.5	N.S.	-	48.0	N.S.	-
CONFLICT	44.0	N.S.	-	46.0	N.S.	-	48.0	N.S.	-
LUNGE	31.0	N.S.	-	21.5	*	2	n.a.	-	-
BITE	41.0	N.S.	-	28.5	N.S.	-	n.a.	-	-
SEIZE	18.5	**	2	15.5	**	2	32.0	N.S.	-
DRAG	12.0	**	2	10.5	**	2	31.0	N.S.	-
STING	19.5	*	2	31.0	N.S.	-	44.0	N.S.	-
CHASE	0.0	***	2	0.0	***	2	n.a.	-	-
FLEE	45.0	N.S.	-	45.0	N.S.	-	n.a.	-	-
GROOM	14.0	**	2	10.5	**	2	9.0	***	2
LOCOMOTION	15.0	**	2	18.0	**	2	18.0	**	2
STILL	19.5	*	1	22.5	*	1	20.5	*	1
ABDOMEN CURLING	46.0	N.S.	-	46.0	N.S.	-	46.0	N.S.	-

and dragged sooner and more often than was an ant of its own species. No differences are present in the durations of the acts SEIZE and DRAG between the species - in fact, they are very similar. More grooming and locomotion are shown, sooner and for longer with *M. rubra*. STILL behaviour was shown more when with its own species, for each of the three measures. Intraspecific fighting was thought, from observations, to lack severity. Indeed, all ants were alive after 24 hours in intraspecific encounters while some were dead as a result of intrageneric combats. The greater activity in intrageneric fighting is also reflected in the pattern of meetings. Meetings occur far more often but for less time with *M. rubra*.

### 2.2.3. Intraspecific and Intergeneric Aggression.

The behaviour of *M. scabrinodis* in intraspecific encounters is compared with its behaviour in encounters with *L. flavus*, *L. umbratus* and *L. niger* in Tables 36, 37 and 38 respectively. The 3 comparisons show similar trends to each other. More fighting (SEIZE and DRAG) occurs and sooner in intraspecific interactions than in ones between different genera in each case. The differences in dragging are not significant for occurrence and latency with respect to the *L. niger* group. Meetings were fewer but for longer periods with its own species than with each *Lasius* due to long bouts of fighting that occurred with the former. Each *Lasius* was approached more often than was its own species. In addition, *L. flavus* was also avoided more. The *Myrmica* showed more THREAT for each measurement towards an enemy of its own species than towards *L. flavus*. THREAT and fighting are positively correlated here. THREAT was shown less often towards its own species than towards *L. niger* and is therefore negatively correlated with fighting in this case. More CONFLICT is shown where *L. umbratus* and *L. niger* are opponents than in con-specific encounters. In each instance, CONFLICT is negatively correlated with fighting. Furthermore, CONFLICT was only shown during



TABLE 36. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *M. scabrinodis*

COMPARED WITH

*M. scabrinodis* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	42.0	N.S.	-	1.5	***	2	n.a.	-	-
AVOID	30.0	N.S.	-	15.0	**	2	n.a.	-	-
MEET	n.a.	-	-	10.0	***	2	0.0	***	1
THREAT	17.5	**	1	18.5	**	1	19.5	*	1
CONFLICT	33.0	N.S.	-	27.5	N.S.	-	29.0	N.S.	-
LUNGE	35.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
BITE	35.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
SEIZE	5.0	***	1	5.0	***	1	5.0	***	1
DRAG	10.0	***	1	10.0	***	1	10.0	**	1
STING	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
CHASE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
FLEE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
GROOM	31.0	N.S.	-	30.0	N.S.	-	29.0	N.S.	-
LOCOMOTION	20.0	*	2	4.0	***	2	12.0	**	2
STILL	32.5	N.S.	-	30.5	N.S.	-	43.0	N.S.	-
ABDOMEN CURLING	1.0	***	2	0.0	***	2	0.0	***	2

TABLE 37. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *M. scabrinodis*

COMPARED WITH

*M. scabrinodis* vs. *L. umbratus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	49.5	N.S.	-	11.0	**	2	n.a.	-	-
AVOID	45.0	N.S.	-	45.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	11.0	**	2	0.0	***	1
THREAT	21.0	*	1	42.5	N.S.	-	35.0	N.S.	-
CONFLICT	25.0	N.S.	-	22.0	*	2	24.5	N.S.	-
LUNGE	47.0	N.S.	-	42.0	N.S.	-	n.a.	-	-
BITE	49.5	N.S.	-	48.5	N.S.	-	n.a.	-	-
SEIZE	17.5	**	1	9.0	***	1	6.5	***	1
DRAG	17.0	**	1	12.0	**	1	12.0	**	1
STING	37.0	N.S.	-	35.0	N.S.	-	34.5	N.S.	-
CHASE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
FLEE	15.0	**	2	15.0	**	2	n.a.	-	-
GROOM	16.0	**	2	16.0	**	2	17.5	**	2
LOCOMOTION	10.0	***	2	7.5	***	2	5.0	***	2
STILL	15.0	**	2	1.0	***	2	26.5	N.S.	-
ABDOMEN CURLING	4.0	***	2	0.0	***	2	1.0	***	2

TABLE 38. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *M. scabrinodis*

COMPARED WITH

*M. scabrinodis* vs. *L. niger*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	47.5	N.S.	-	6.5	***	2	n.a.	-	-
AVOID	30.0	N.S.	-	25.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	10.0	***	2	0.0	***	1
THREAT	42.5	N.S.	-	17.5	**	2	30.0	N.S.	-
CONFLICT	24.5	N.S.	-	3.5	***	2	7.0	***	2
LUNGE	35.5	N.S.	-	45.0	N.S.	-	n.a.	-	-
BITE	49.5	N.S.	-	45.0	N.S.	-	n.a.	-	-
SEIZE	18.0	**	1	14.5	**	1	7.5	***	1
DRAG	27.0	N.S.	-	25.0	N.S.	-	22.0	*	1
STING	38.0	N.S.	-	39.0	N.S.	-	36.0	N.S.	-
CHASE	20.0	*	2	20.0	*	2	n.a.	-	-
FLEE	45.0	N.S.	-	45.0	N.S.	-	n.a.	-	-
GROOM	31.0	N.S.	-	42.0	N.S.	-	38.5	N.S.	-
LOCOMOTION	19.5	*	2	12.0	**	2	18.0	**	2
STILL	44.5	N.S.	-	30.0	N.S.	-	39.5	N.S.	-
ABDOMEN CURLING	3.0	***	2	16.0	**	2	21.0	*	2

meetings with alien *M. scabrinodis* whereas with the *Lasius* species much was shown in the INTER-MEET periods (see Figure 22 page 129). *M. scabrinodis* chases *L. niger* and flees from *L. umbratus* more than it does from its own species.

The passive postures, STILL and ABDOMEN-CURLING, were sustained after a meeting with the 3 *Lasius* species far more than with an alien of its own species (see Figure 21 , page 128).

#### 2.2.4. Intragenetic and Intergeneric Aggression.

The behaviour of *M. scabrinodis* towards *M. rubra* is compared with its behaviour to *L. flavus*, *L. umbratus* and *L. niger* in Tables 39, 40 and 41 respectively. It can be seen, in all 3 comparisons, that there are striking differences between Intra-genetic and Intergeneric encounters. Far more aggression is shown to *M. rubra* than to each of the *Lasius* species. Significant differences can be seen in the acts SEIZE, DRAG, and STING for each of the 3 behavioural measures. The 2 passive acts, STILL and ABDOMEN-CURLING, are shown correspondingly far less often, for less time and later on in intra-genetic encounters. The differences in the sustainment periods of these 2 postures after a meeting are shown in Figure 21 page 128. Threatening behaviour is shown sooner, more often and for longer with *M. rubra* than with *L. flavus*. THREAT and fighting are thus positively correlated. More lunging and biting are also done with the former. No significant differences are present in THREAT, LUNGE and BITE in comparisons involving *L. umbratus* and *L. niger*. Scores for CONFLICT are higher with *L. umbratus* and *L. niger* than with *M. rubra*. CONFLICT is negatively correlated with fighting. Further, while CONFLICT is often shown in the INTER-MEET periods with *Lasius* opponents it is usually only shown during meetings with *M. rubra* (see page 129). Because long durations of combat occur with *M. rubra*, meetings are longer but fewer in number than with the *Lasius* species. *M. rubra* is chased sooner and more often than are both *L. flavus* and *L. umbratus* but not more than *L. niger*

TABLE 39. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *M. rubra*.

COMPARED WITH *M. scabrinodis* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	47.0	N.S.	-	43.5	N.S.	-	n.a.	-	-
AVOID	41.0	N.S.	-	34.5	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	22.5	*	2	3.0	***	1
THREAT	16.0	**	1	10.5	**	1	12.0	**	1
CONFLICT	25.0	N.S.	-	23.5	N.S.	-	32.0	N.S.	-
LUNGE	15.0	**	1	15.0	**	1	n.a.	-	-
BITE	15.0	**	1	15.0	**	1	n.a.	-	-
SEIZE	0.0	***	1	0.0	***	1	0.0	***	1
DRAG	0.0	***	1	0.0	***	1	0.0	***	1
STING	5.0	***	1	0.0	***	1	0.0	***	1
CHASE	0.0	***	1	0.0	***	1	n.a.	-	-
FLEE	50.0	N.S.	-	45.0	N.S.	-	n.a.	-	-
GROOM	14.0	**	1	21.0	*	1	20.0	*	1
LOCOMOTION	41.0	N.S.	-	49.5	N.S.	-	37.0	N.S.	-
STILL	6.5	***	2	17.0	**	2	15.0	**	2
ABDOMEN CURLING	2.0	***	2	0.0	***	2	0.0	***	2

TABLE 40. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *M. rubra*

COMPARED WITH

*M. scabrinodis* vs. *L. umbratus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	40.0	N.S.	-	24.0	N.S.	-	n.a.	-	-
AVOID	44.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	13.0	**	2	0.0	***	1
THREAT	24.0	N.S.	-	23.5	N.S.	-	29.0	N.S.	-
CONFLICT	13.0	**	2	19.5	*	2	27.0	N.S.	-
LUNGE	34.0	N.S.	-	25.0	N.S.	-	n.a.	-	-
BITE	39.0	N.S.	-	25.5	N.S.	-	n.a.	-	-
SEIZE	0.0	***	1	1.0	***	1	1.0	***	1
DRAG	0.5	***	1	0.0	***	1	0.0	***	1
STING	14.5	**	1	9.5	***	1	6.0	***	1
CHASE	10.0	***	1	3.0	***	1	n.a.	-	-
FLEE	15.0	**	2	24.5	N.S.	-	n.a.	-	-
GROOM	23.0	*	1	24.0	N.S.	-	35.0	N.S.	-
LOCOMOTION	26.0	N.S.	-	25.0	N.S.	-	12.0	**	2
STILL	0.0	***	2	1.0	***	2	4.0	***	2
ABDOMEN CURLING	0.0	***	2	1.0	***	2	2.0	***	2

TABLE 41. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *M. rubra*

COMPARED WITH

*M. scabrinodis* vs. *L. niger*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	39.5	N.S.	-	24.0	N.S.	-	n.a.	-	-
AVOID	43.0	N.S.	-	47.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	19.5	*	2	3.0	***	1
THREAT	45.5	N.S.	-	48.0	N.S.	-	32.5	N.S.	-
CONFLICT	7.0	***	2	3.5	***	2	16.0	**	2
LUNGE	50.0	N.S.	-	36.0	N.S.	-	n.a.	-	-
BITE	38.5	N.S.	-	27.5	N.S.	-	n.a.	-	-
SEIZE	9.0	***	1	2.5	***	1	4.0	***	1
DRAG	5.0	***	1	5.0	***	1	8.0	***	1
STING	14.0	**	1	22.5	*	1	17.0	**	1
CHASE	38.0	N.S.	-	29.5	N.S.	-	n.a.	-	-
FLEE	49.5	N.S.	-	49.5	N.S.	-	n.a.	-	-
GROOM	24.0	N.S.	-	29.5	N.S.	-	34.0	N.S.	-
LOCOMOTION	44.5	N.S.	-	28.0	N.S.	-	15.0	**	2
STILL	10.5	**	2	38.5	N.S.	-	13.5	**	2
ABDOMEN CURLING	5.5	***	2	15.0	**	2	15.0	**	2

### 2.3. Discussion

The literature often reports *M. scabrinodis* living in close association with *L. flavus* but less so with other species. Chapter 3 investigated the former relationship and showed that although the *Myrmica* will threaten it will not attack *L. flavus* in pair encounters. Results from this chapter show that, in the same controlled conditions, *M. scabrinodis* behaves in different ways to other species. The behaviour was most similar to the 3 *Lasius* opponents. Of the 3 aggression was believed to be fiercest to *L. niger* where a high level of THREAT and some fierce and fatal fights occurred. This is in contrast to the low level of attraction and aggression shown by *M. rubra* towards *L. niger* in the experiments of De Vroey (1979). *L. niger* frequently avoided *M. scabrinodis* by its agility and speed, particularly in initial meetings. This avoidance behaviour would seem to be a common tactic employed by *L. niger* as it has been recorded in individuals upon meeting *T. caespitum* (Brian, 1966) and *M. rubra* (De Vroey, 1979). *M. scabrinodis*, unlike *M. rubra*, exhibits a marked attraction and a high level of chasing behaviour towards *L. niger*. The responses of the 2 *Myrmica* towards an alien are therefore quite different. *M. scabrinodis* and *L. niger* occur in the same habitat, they forage above ground, and meetings are probably frequent. *L. niger* may dominate a food site by its aggressive behaviour (De Vroey, 1978). *Myrmica* are eaten by *L. niger* (Pontin, 1961; Brian, 1965). The differences in aggression seen in encounters with *L. flavus* and *L. niger* would explain why *Myrmica* nests do not occur as near to *L. niger* as they do towards *L. flavus* (Pontin, 1969). The behaviour of *M. scabrinodis* towards *L. umbratus* is of particular interest as this species, like *L. flavus*, is subterranean. Both *Lasius* are sometimes found in the same habitat (Carey and Diver, 1937) and they may even occur beneath the same stone (Pontin, 1963). *L. umbratus* showed the same willingness to approach and attack the *Myrmica* at each meeting as



*L. flavus* did and in this respect is different from *L. niger* whose behaviour was more variable. The continual attraction of *L. umbratus* to an opponent would support the alarm/defence strategy proposed for a subterranean species earlier (see page 108). The response of the *Myrmica* to *L. umbratus* was more like that to a *L. flavus* than a *L. niger* opponent. For example, the rather stereotyped passive postures were shown more and sustained for longer periods than with *L. niger*. *L. umbratus* is usually larger than *L. flavus* (Donisthorpe, 1927). It was seen to move and 'unbalance' the *Myrmica* by its pulling actions in a way that *L. flavus* did not. The apparent difference in strength between *L. umbratus* and *L. flavus* may be responsible for the differences in behaviour of the *Myrmica* towards the 2 species. Furthermore, *L. umbratus* sometimes employed its gaster in attacks while *L. flavus* did not - an action, which induced fleeing behaviour. Potent secretions of the ant's Dufours gland have been demonstrated by Bergstrom and Lofqvist (1972). The *Myrmica* is less willing to remain passive as it did in pair encounters with *L. flavus* and such differences at the individual level may influence colony interactions and the formation of compound nests.

The fierce fighting seen between individuals of *M. scabrinodis* and *M. rubra* may reflect the intolerance of their colonies to each other in the field. Both species are often found in the same habitat and probably compete for resources. *M. rubra* is considered to be one of the most aggressive *Myrmica* and *M. scabrinodis* one of the least war-like (Farren-White, 1883; Donisthorpe, 1913). However in these experiments *M. scabrinodis* often approached, chased and attacked its opponent. The fighting superiority of *M. rubra* was seen in the 4:1 ratio of deaths that resulted. The large number of deaths was expected as both ants used their gasters liberally in combat.

The *M. scabrinodis* always approached and seized an alien of their

own species for long durations. The marked lack of severity of such attacks and the uninjured condition of all combatants, even after 24 hours, is interesting. Donisthorpe (1927) notes that intraspecific fighting occurs in this species but that mortalities are much less than in *M. rubra* or *M. ruginodis*.

The 'jaw-to-jaw' seizing, large extent of antennal communication and readiness of one ant to move in unison with the pulling motions of the opponent suggest a system for avoiding fierce combat and possibly for assessing the opponent's strength or motivation. The dragging behaviour will function to remove an intruder from an area with minimal damage to both individuals. Ritualized combats have been described in the honey-pot ants (Holldobler, 1976b). Indeed, it is disadvantageous for colonies of the same or different species to have continual battles and a degree of stabilization probably occurs in most cases in the wild. Many mechanisms are employed by ants to avoid aggressive encounters such as foraging rhythms and strategies, trunk trails, etc. Dominance hierarchies and mosaic distributions are well known. (Brian, 1958; Majer, 1972). The submissive response of *M. scabrinodis*, described earlier, is yet another strategy used at the individual level for avoiding a fight.

The STILL and ABDOMEN-CURLING postures of *M. scabrinodis* were often performed and sustained, with *Lasius* opponents but rarely with opponents of its own genus, with the exception of the STILL response in intraspecific encounters. Interactions with the latter were more intense. The submissive posture may be ineffective in such situations or the animal may be more highly motivated to compete. It is certainly disadvantageous for the ant to remain in a 'neutral' area where danger exists. The CONFLICT response was performed more in intra-rather than inter-generic

encounters. If CONFLICT serves to attract congeners, as is believed in nest interactions with *L. flavus*, then it will be done so less in dangerous areas.

It is believed from Gauze's law that "2 species with similar ecology cannot live together in the same place" (Gauze, 1934). Interpretations of the hypothesis have been discussed by Gilbert *et al* (1952) and Hardin (1960). The more taxonomically and ecologically similar the species the greater the competition between them should be. Intra-specific competition has been found to be greater than interspecific competition in ants by Pontin (1961). Aggression is often related to competition although ants may compete in many ways other than by combat. Holldobler (1976a) and Brian (1965) have shown intraspecific aggression to be greater than interspecific aggression. The hostility between closely-related species is often great (Wilson, 1951; Way, 1953). Observations on the interactions between *M. scabrinodis* and 5 different ant species have enabled a detailed comparison of intra- and interspecific aggression between individuals to be made. The experiments clearly show that intraspecific aggression is less fierce than intrageneric aggression. Further, while some deaths resulted in intergeneric combats which were sporadic but fierce, none occurred when *M. scabrinodis* fought with aliens of its own species. De Vroey (1979) has, concurrently, obtained similar results for *M. rubra*. This author considers the aggressiveness in terms of the monogyny/polygyny status of the species - polygynous colonies, such as *M. rubra* and *M. scabrinodis*, are believed to be less aggressive than monogynous ones. Similar findings have been reported by Talbot (1948), Brian *et al* (1949), Marikowski (1963) and Pisarski (1972). Gilbert *et al* (1952) state that competition can be ascertained only by a consideration of changes in the relative sizes of populations. It is clear from the experiments of this study in carefully controlled

conditions that one cannot necessarily relate the level of aggression seen in ants to the degree of competition or taxonomic relationship between species. There are, no doubt, many ecological examples which would show this.

The experiments of Chapter 4 are taken to evaluate the use of the 3 measurements of behaviour, occurrence, duration and latency, and to assess the value of the 16 responses observed. When the 3 measurements are examined it is found that the relative importance of each one may differ depending on the type of encounter analysed. One example will be considered. *M. scabrinodis* seizes both alien *M. scabrinodis* and *M. rubra* opponents during combat. Figure 24 shows that, with respect to the former, scores for occurrence are low and duration high, but with the latter both are relatively high. This is a reflection of the higher intensity of the interactions with the latter. Clearly then, both measurements are needed to describe the behaviour and one alone would give misleading results.

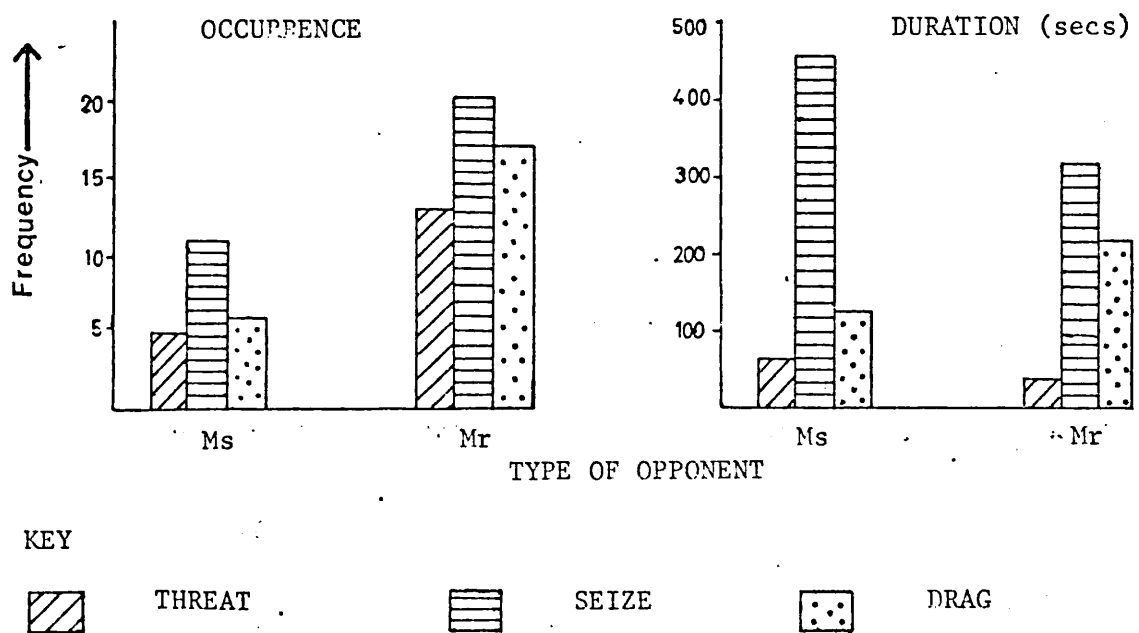


Figure 24. Mean scores for 3 aggressive responses shown by individuals of *M. scabrinodis* in pair encounter experiments with alien *M. scabrinodis* and *M. rubra* (n = 10).

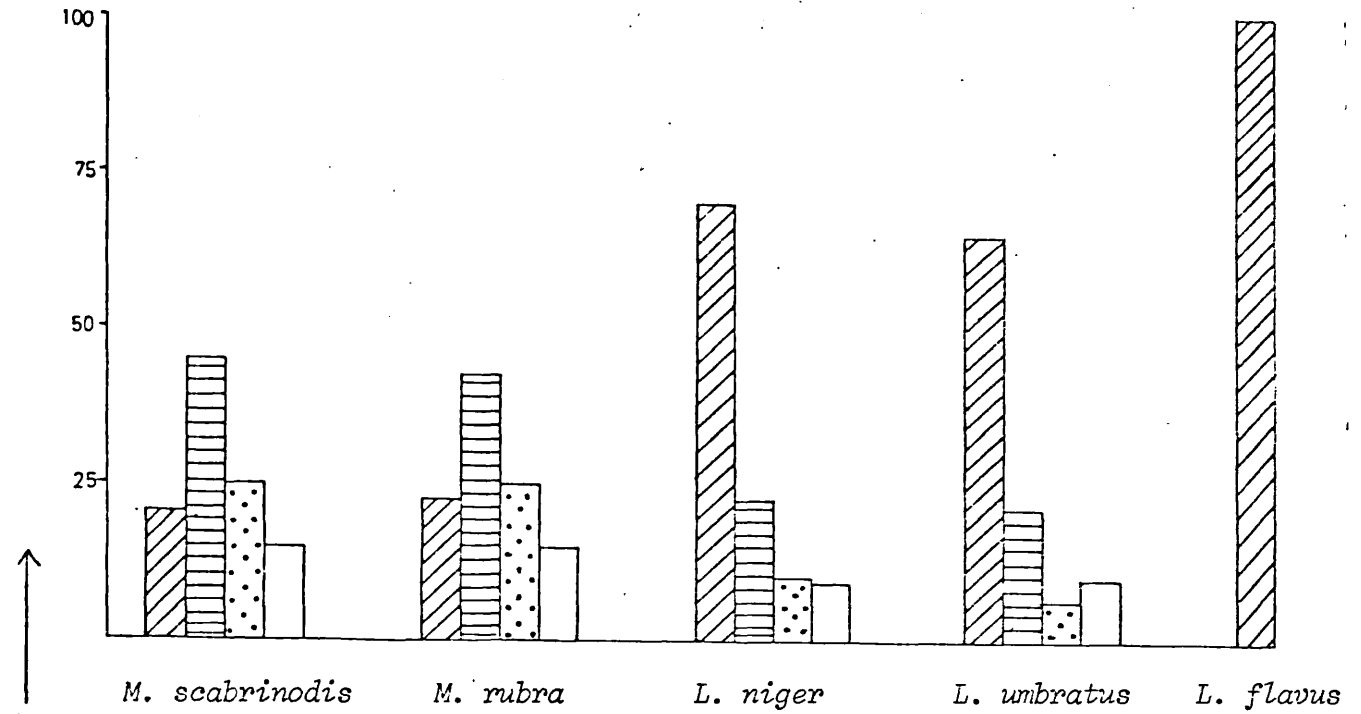
The total number of significant differences from all comparisons of pair-encounter experiments from the 3 experimental chapters are shown below in Table 42 for each of the 3 measurements.

TABLE 42. Total number of significant differences from all pair encounter experiments.

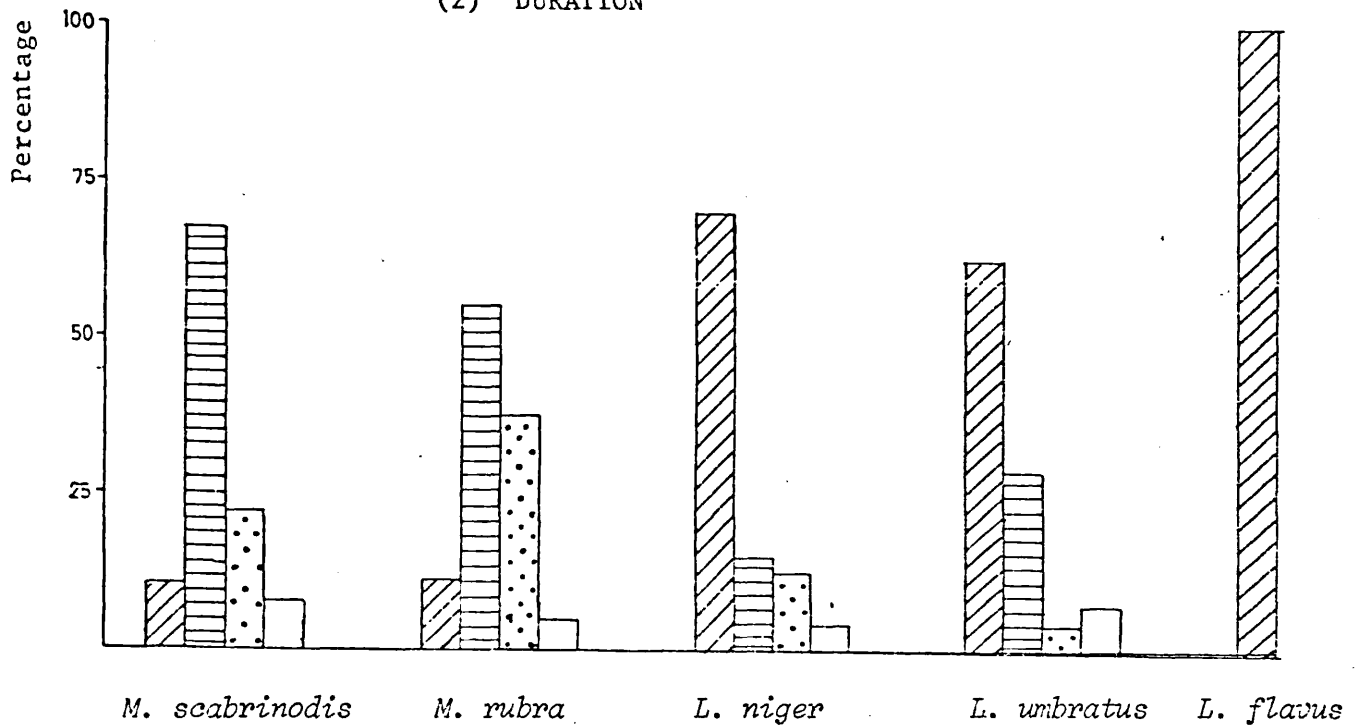
	Occurrence	Duration	Latency
Frequency	177	137	138

There were many cases where each measurement showed a significant effect when the other 2 did not and, therefore, at such times they are of particular value. Latency is, perhaps, less valuable than occurrence and duration but it provides additional information and it is quick and easy to record. 16 responses were recorded in encounters in order to obtain a full, quantitative analysis of behavioural interactions. Aggressive acts actually connected with fighting are much fewer in number. The most important of these are probably THREAT, SEIZE, DRAG and STING. These 4 acts are considered first. It was seen in Chapter 4 that the behaviour of *M. scabrinodis* depends very much on the type of opponent. This is particularly true with respect to these 4 aggressive acts. Figures 25(1) and (2) compare the 4 aggressive responses of *M. scabrinodis* as a percentage of each other in encounters with 5 different species. The most obvious difference is that the ant tends to seize *Myrmica* opponents but to threaten *Lasius* ones. Percentage differences in other acts are also apparent. This type of analysis has serious limitations as it does not compare actual amounts of aggression between species. For example, the ant threatens *L. niger* much more than *L. flavus* yet the former's percentage score is lower. Clearly, any analysis of aggression must consider more than one aggressive response. All of the above 4 are felt necessary to quantify aggression in ants. Stinging is performed relatively less than the other 3 acts, particularly when duration is used as a measurement, yet it is important to an analysis

(1) OCCURRENCE



(2) DURATION



KEY

- THREAT
- SEIZE
- DRAG
- STING

FIGURE 25. The frequencies (1) and durations(2) of 4 aggressive responses, expressed as a percentage of their combined totals, shown by *M. scabrinodis* in pair encounters with 5 different species.

because of its serious consequences. Dragging is of value as it probably involves a higher level of motivation than seizing (Wallis, 1962) and thus indicates the intensity of interactions. Dragging (active pulling during combat) must be distinguished from carrying where the level of activity is much less. Threat has been positively correlated with aggressive acts such as seizing, dragging and stinging (Wallis, 1962; De Vroey, 1978). Threat is also statistically correlated with seizing ( $r_s = 0.83, p < 0.01$ )\* in encounters between *M. scabrinodis* and *M. rubra* in these experiments. The association of threat and fighting is quite obvious and has been discussed by both Wallis and De Vroey. However, threat is not necessarily just a sequel to attack, for the posture may be a reflection of opposing tendencies or it may convey a warning to its opponent. Thus, a high level of threat does not necessarily mean a similarly high amount of fighting. One example is taken to illustrate this - *M. scabrinodis* shows a great deal more threat towards *L. niger* but seizes and drags the ant much less than it does both alien *M. scabrinodis* and *M. rubra*. Indeed, in such cases threat and fighting appear to be negatively correlated. Nevertheless, threat is a very useful response for measuring aggression, particularly in encounters between species where combat is infrequent.

Scores for LUNGE and BITE were low in most types of encounter investigated and the acts are thus of little value in measuring aggression. CONFLICT has been shown to be distinct from THREAT. It is performed by the animal in different amounts and at different times. The response is a very important one in the behaviour of *M. scabrinodis*, particularly in encounters with *Lasius* opponents where less fighting occurs than with *Myrmica* ones. The frequency and duration that an ant approaches or avoids, chases or flees, shows locomotion, or grooms in a given time period depends on the number and duration of combats. As fighting is very variable among different species so are the scores of other responses.

---

\* Spearman rank correlation coefficient.

When an ant is fighting it cannot perform other behaviour, although it may wish to. For example, a badly injured ant may wish to groom but cannot do so while being attacked. Ants engaged in combats for long periods (e.g. intraspecific encounters) will meet less frequently and thus have less opportunity to approach or avoid, than if little fighting occurred. Indeed, measuring the occurrence and durations of meetings, and to a lesser extent locomotion, provides very useful information on the type of interactions in encounters. Measuring responses such as approach, avoid, chase and flee is very useful for it further quantifies subjective observations. Acts must be clearly defined. For example the gaster of *M. scabrinodis* was curled beneath the body in at least 3 different ways. The first was termed ABDOMEN-CURLING and the second stinging (although eversion of the sting was not examined). The third was also termed stinging although it differed from the second in the quickness of the action and the conditions in which it was seen. THREAT and CONFLICT have not been given a 'separate' identity by other workers yet the experiments clearly show that they are different responses. In recent years there has been a pronounced trend in behavioural studies towards statistical analysis. The investigations of this study show that there is a place, indeed a need, to qualify such figures with accurate descriptive accounts.



CHAPTER 5

INDIVIDUAL INTERACTIONS BETWEEN  
6 MYRMICA SPECIES AND L. FLAVUS.

## 1. Introduction and Method.

British species of the genus *Myrmica* are thought to be closely related. Many of them may occur in the same habitat (Brian *et al* 1949; Brian, 1952, 1955, 1956a, b. 1958). The ecology and distribution of <sup>the</sup> genus are given — by Donisthorpe (1927) and Gaspar (1971). Elmes (1975) has done a population study on the genus and proposes a spatial relationship of the species in terms of warmth and humidity requirements. Species of the genus are often compared in terms of their morphological characters. A revision of the North American *Myrmica* is given by Weber (1947). To date, no quantitative and comparative analysis of their behaviour has been made. The small size of the British genus lends itself to such a comparison.

The following chapter investigates the interspecific behaviour of 6 species of the genus *Myrmica* towards the same type of opponent, *L. flavus*. The behavioural status of the species is then compared with the taxonomic one. The species studied were: *M. sabuleti*, *M. schencki*, *M. rubra*, *M. ruginodis* and *M. sulcinodis*. The responses shown by each species in pair encounter experiments with *L. flavus* were examined following the 'General Method' (page 7 ). The behaviour of *M. scabrinodis* towards *L. flavus* is given in 2.2.1. (page 30 ).

## 2. Results.

### 2.1. Interactions.

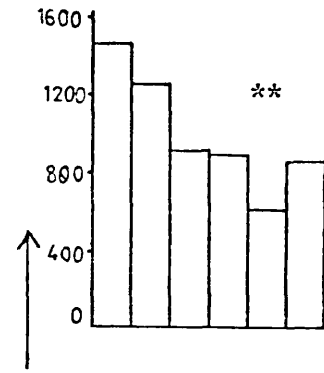
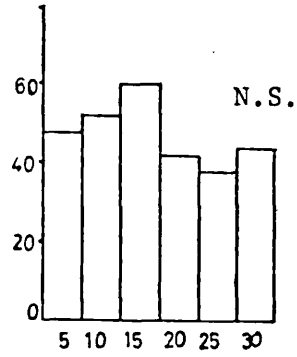
#### 2.1.1. *M. sabuleti* vs. *L. flavus*.

Mean scores for the acts shown by *M. sabuleti* in encounters with *L. flavus* are given in Table 43. The behaviour of *M. sabuleti* was fairly constant throughout the encounter and in each replicate trial. Only 2 acts, MEET and LOCOMOTION, changed significantly with time (see Figure 26 a. and b respectively). The temporal patterning of all responses is analysed in the Appendix, (Table 13).

TABLE 43. Mean Scores for the responses shown by individuals of *M. sabuleti* in pair encounters with *L. flavus*. (n = 10).

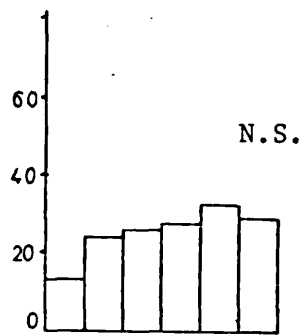
RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	0.9	n.a.
AVOID	0.6	n.a.
MEET	27.7	589.2
THREAT	0.1	0.4
CONFLICT	1.5	83.6
LUNGE	0.0	n.a.
BITE	0.0	n.a.
SEIZE	0.0	0.0
DRAG	0.0	0.0
STING	0.0	0.0
CHASE	0.0	n.a.
FLEE	0.0	n.a.
GROOM	1.0	4.4
LOCOMOTION	14.9	371.8
STILL	18.9	1279.0
ABDOMEN CURLING	2.0	57.4

(a) MEET

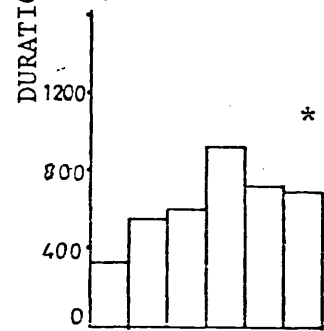


OCCURRENCE ↑

(b) LOCOMOTION



DURATION (secs) ↑



TIME (5 min. intervals) →

FIGURE 26. Temporal patterning of the responses shown by *M. sabuleti* in 30 minute pair encounters with *L. flavus*. (see KEY, page 50).

Each time that the ant met the opponent the STILL response was shown. The response was often sustained throughout the meeting and after the opponent had departed (see Figure 30 page 167). Duration scores for the STILL response are almost twice that of the MEET category (Table 43). The ABDOMEN-CURLING response was adopted infrequently and by only a proportion of the ants. The gaster was often only partially curled under the body. The aggressive acts LUNGE, BITE, SEIZE, DRAG, STING and CHASE were never shown. Fighting did not take place in any encounter and all ants were alive after 24 hours. APPROACH, AVOID, THREAT and GROOM rarely occurred. A small amount of CONFLICT was shown by only a proportion of the animals.

#### 2.1.2. *M. schencki* vs. *L. flavus*.

Mean scores for the acts shown by *M. schencki* in encounters with *L. flavus* are given in Table 44. Two of these acts, LOCOMOTION and STILL, change significantly with time (see Figure 27a, and b). The temporal patterning of all acts is analysed in the Appendix, (Table 14).

The behaviour of *M. schencki* towards the *Lasius* seemed extremely similar to that of *M. sabuleti* in almost every respect. The STILL posture was performed at each meeting and sustained into the INTER-MEET period (see Figure 30 page 167). ABDOMEN-CURLING was rarely seen. LOCOMOTION occurred in a slow deliberate manner. The aggressive acts LUNGE, BITE, SEIZE, DRAG, STING and CHASE were not shown. Fighting did not take place and all animals were alive after 24 hours. The responses AVOID, THREAT, CONFLICT, FLEE and GROOM were performed very little.

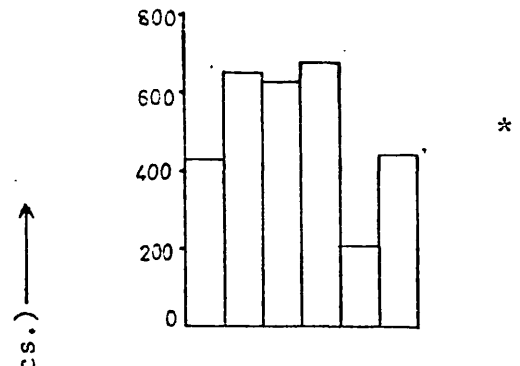
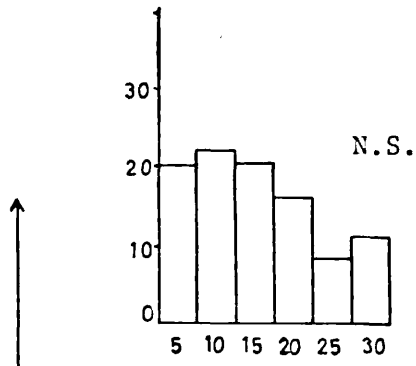
#### 2.1.3. *M. ruginodis* vs. *L. flavus*.

Mean scores for the acts shown by *M. ruginodis* in encounters with *L. flavus* are given in Table 45. None of the acts changed in pattern throughout the experimental period (see Appendix, Table 16).

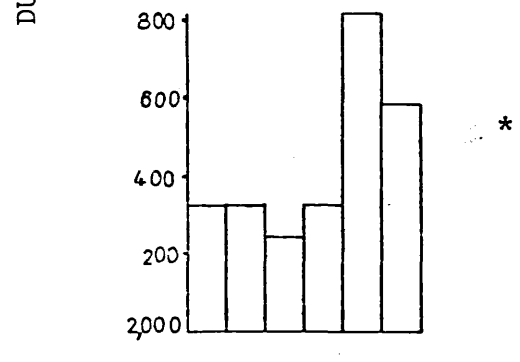
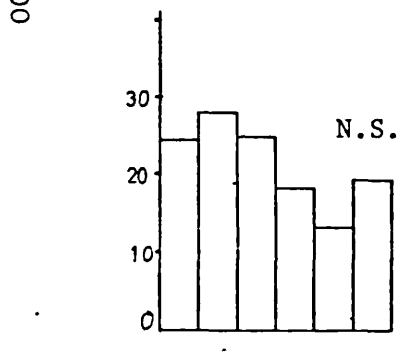
TABLE 44. Mean Scores for the responses shown by individuals of *M. schencki* in pair encounters with *L. flavus*. (n = 10)

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	2.8	n.a.
AVOID	0.5	n.a.
MEET	22.8	868.6
THREAT	0.1	0.2
CONFLICT	0.9	16.0
LUNGE	0.0	n.a.
BITE	0.0	n.a.
SEIZE	0.0	0.0
DRAG	0.0	0.0
STING	0.0	0.0
CHASE	0.0	n.a.
FLEE	0.8	n.a.
GROOM	0.4	5.6
LOCOMOTION	10.1	305.4
STILL	12.5	1444.6
ABDOMEN CURLING	0.2	3.4

(a) LOCOMOTION



(b) STILL



TIME (5 min intervals) →

FIGURE 27. Temporal patterning of the responses shown by *M. schencki* in 30 minute pair encounters with *L. flavus*. (see KEY, page 50 ).

TABLE 45. Mean Scores for the responses shown by individuals of *M. ruginodis* in pair encounters with *L. flavus*. (n = 10).

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	0.8	n.a.
AVOID	2.4	n.a.
MEET	31.1	1043.4
THREAT	1.1	9.8
CONFLICT	0.2	2.4
LUNGE	0.8	n.a.
BITE	0.4	n.a.
SEIZE	1.4	32.0
DRAG	1.1	36.2
STING	1.1	60.4
CHASE	0.3	n.a.
FLEE	0.4	n.a.
GROOM	6.3	46.4
LOCOMOTION	30.9	643.2
STILL	33.3	468.0
ABDOMEN CURLING	23.9	436.6



The STILL act was performed in most meetings in the encounter. The ABDOMEN-CURLING response was also shown a great deal. The gaster was curled and sustained only when actually examined by the opponent. Consequently it was often only briefly sustained. The ant continually ensured that the tip of the gaster was directed away from the opponent. Both the STILL and ABDOMEN-CURLING acts were rarely sustained after a meeting (see Figures 30 and 31 ) and LOCOMOTION usually began immediately. LOCOMOTION was performed at a relatively fast rate and for long periods. Long bouts of grooming were done between periods of LOCOMOTION. The *Myrmica* avoided and fled from the opponent particularly in initial interactions. Little THREAT and CONFLICT were performed. Only 2 individuals fought with the *Lasius*. All ants when selected initially were considered to be of the most aggressive category! Fighting was fierce when it did occur and gasters were employed. Two *Lasius* were killed and their opponents showed signs of injury. All ants in the 8 remaining trials were alive after 24 hours.

#### 2.1.4. *M. rubra* vs. *L. flavus*.

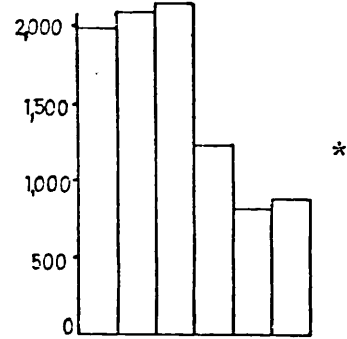
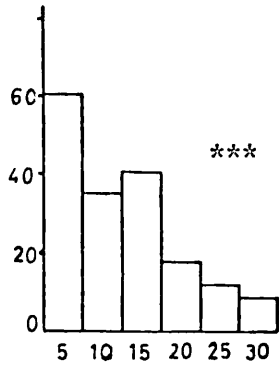
Mean scores for the acts shown by *M. rubra* in encounters with *L. flavus* are given in Table 46. Acts that changed significantly with time are illustrated in Figure 28. Temporal patterning of all acts is analysed in the Appendix, Table 15).

The ants showed a number of different responses on meeting the opponent. Activity ceased and the STILL response was shown in many interactions. ABDOMEN-CURLING was sometimes performed but sustained for only short durations. Often, the gaster was only partly curled beneath the body. Both 'passive' postures show a temporal patterning. Neither posture was sustained after the opponent had departed (see Figures 30 and 31 ). LOCOMOTION was usually performed at a relatively

TABLE 46. Mean Scores for the responses shown by individuals of *M. rubra* in pair encounters with *L. flavus*. (n = 10).

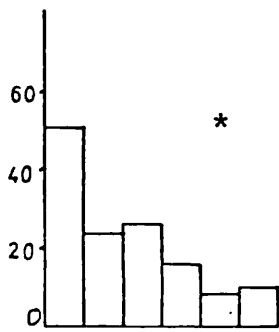
RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	0.9	n.a.
AVOID	5.9	n.a.
MEET	17.7	801.4
THREAT	6.2	227.0
CONFLICT	2.1	19.2
LUNGE	0.5	n.a.
BITE	0.0	n.a.
SEIZE	1.0	18.0
DRAG	2.9	34.0
STING	3.8	31.0
CHASE	0.0	n.a.
FLEE	2.3	n.a.
GROOM	0.3	0.6
LOCOMOTION	13.0	311.4
STILL	14.1	391.6
ABDOMEN CURLING	5.5	22.8

MEET

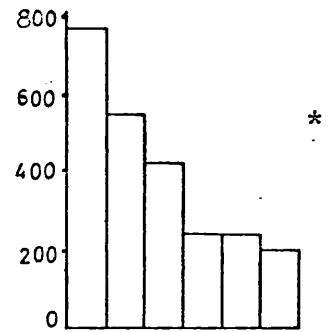


LOCOMOTION

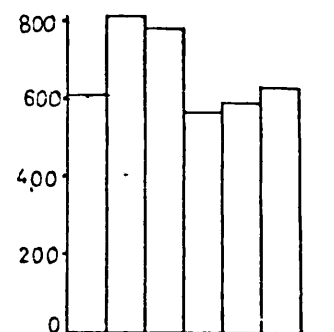
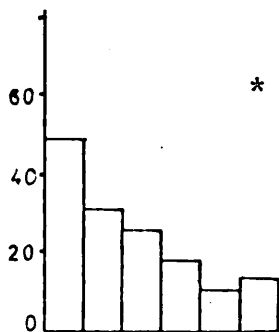
OCCURRENCE ↑



DURATION (secs) ↑



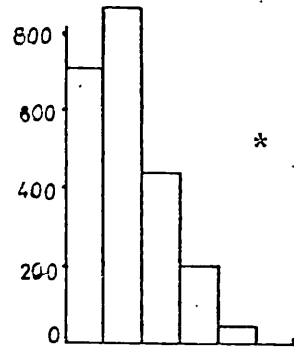
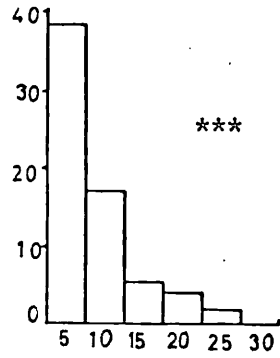
STILL



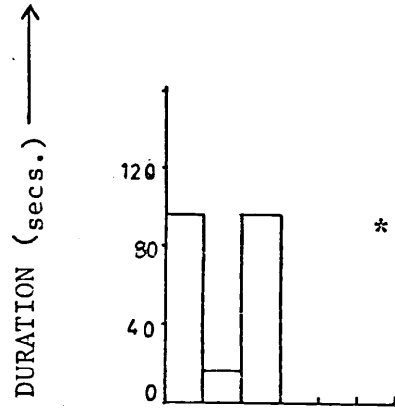
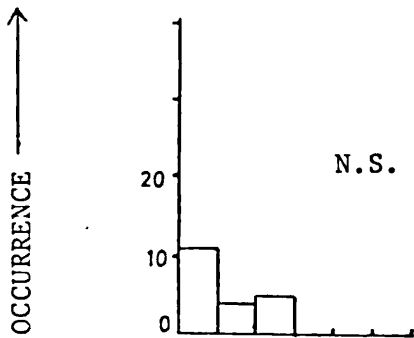
TIME INTERVAL (5 min. periods) →

FIGURE 28(a) Temporal patterning of the responses shown by *M. rubra* in 30 minute pair encounters with *L. flavus*. (see KEY, page 50 ).

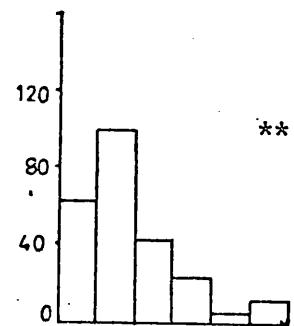
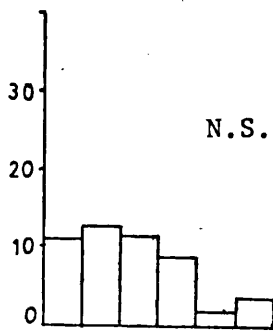
THREAT



CONFLICT



ABDOMEN CURLING



TIME INTERVAL (5 min. periods) →

FIGURE 28(b). Temporal patterning of the responses shown by *M. rubra* in 30 minute pair encounters with *L. flavus*. (see KEY, page 50 ).

fast rate and it began immediately after the meeting. LOCOMOTION was greatest initially and decreased with time. The ant often avoided and fled from the opponent. Little APPROACH occurred and CHASE was not seen.

Although the *Myrmica* were passive in many interactions, at times much aggression was shown. All ants threatened the *Lasius* a great deal. Some CONFLICT was also performed. Both THREAT and CONFLICT were exhibited significantly more in the initial minutes of the encounter. Most of the ants attacked the *Lasius* at some stage during the encounter. The fighting was fierce. Seizing, dragging and stinging actions were frequent and for long durations. Some deaths occurred in the experimental period. 7 *Myrmica* and 8 *Lasius* were dead after 24 hours.

#### 2.1.5. *M. sulcinodis* vs. *L. flavus*.

Mean scores for the acts shown by *M. sulcinodis* in encounters with *L. flavus* are given in Table 47. The temporal patterning of these acts is analysed in the Appendix (Table 1). Two of these acts, MEET and LOCOMOTION, show a significant change. The durations of both responses decrease with time (see Figure 29a, and b respectively).

The *Myrmica* exhibited a variety of responses in interactions. The STILL and ABDOMEN-CURLING acts were adopted in some meetings. Both postures were rarely sustained after a meeting (see Figures 30 and 31) and LOCOMOTION soon began. The ants performed LOCOMOTION, at times, with the abdomen held beneath the body and with the jaws opened wide. The behaviour occurred directly after a meeting and lasted for some 6 seconds (see Table 47). The response was not observed in other *Myrmica* with possibly the exception of *M. ruginodis* where it was seen occasionally and briefly.

Although the ants were passive in some meetings, a high level of

TABLE 47. Mean Scores for the responses shown by individuals of *M. sulcinodis* in pair encounters with *L. flavus*. (n = 10).

RESPONSES	OCCURRENCE	DURATION (Secs)
APPROACH	2.9	n.a.
AVOID	2.6	n.a.
MEET	15.8	932.0
THREAT	9.8	124.0
CONFLICT	4.1	43.2
LUNGE	5.0	n.a.
BITE	7.5	n.a.
SEIZE	10.2	166.0
DRAG	9.4	275.6
STING	7.2	95.4
CHASE	1.4	n.a.
FLEE	1.4	n.a.
GROOM	3.3	35.4
LOCOMOTION	11.8	410.8
STILL	6.9	183.6
ABDOMEN CURLING	2.1	24.8
Ab.C IN LOCOMOTION	4.4	25.2

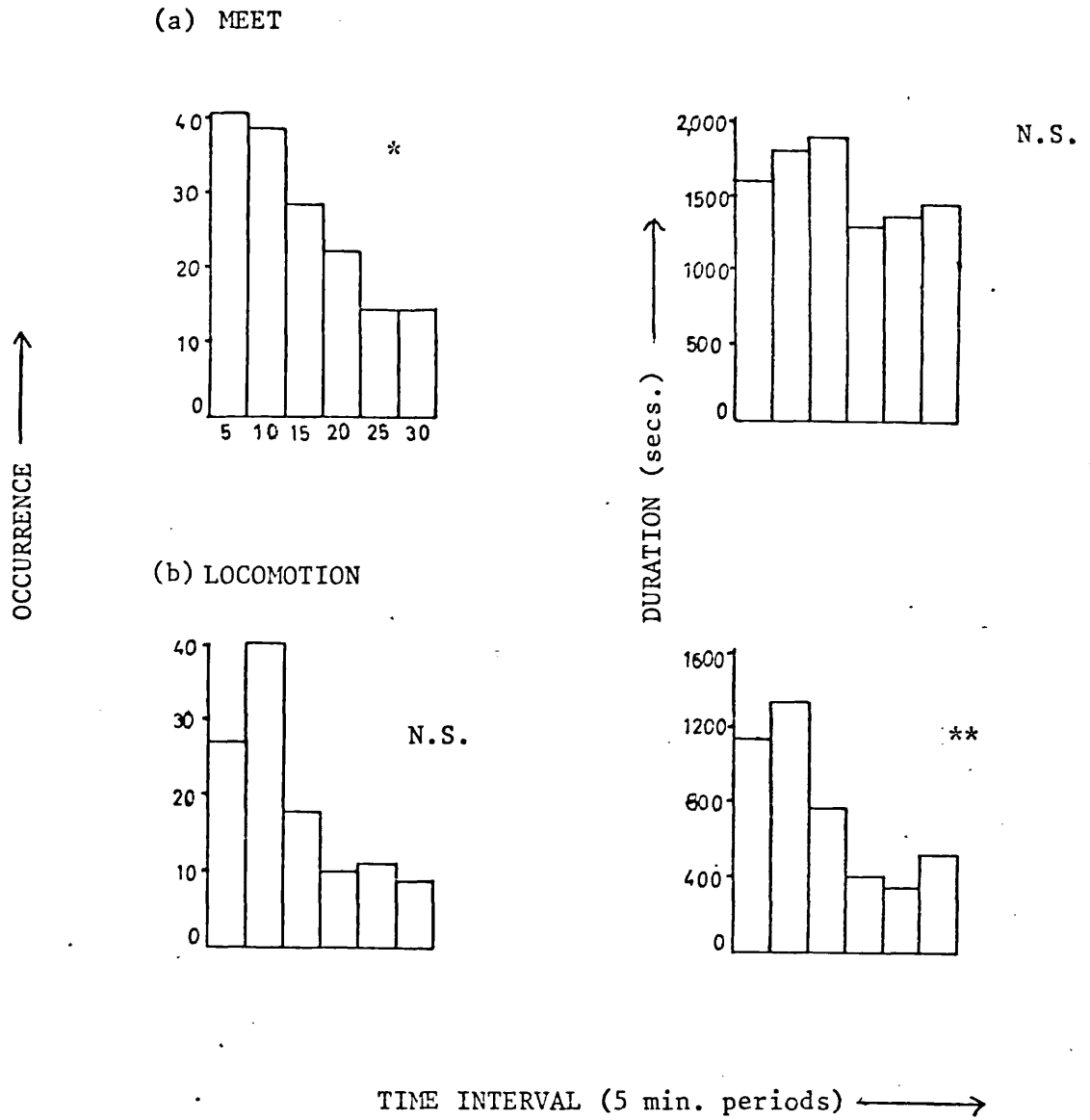
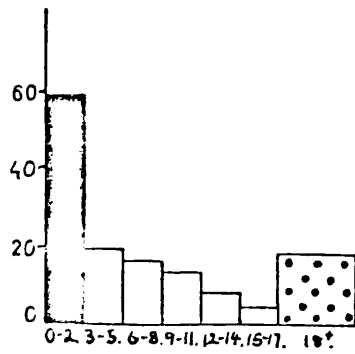
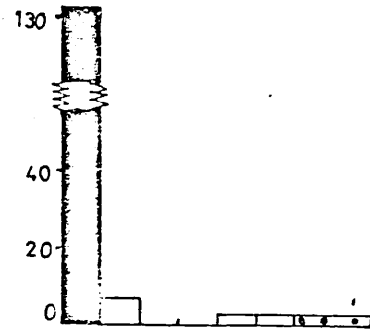


FIGURE 29. Temporal patterning of responses shown by *M. sulcinodis* in 30 minute pair encounters with *L. flavus* (see KEY, page 50 ).

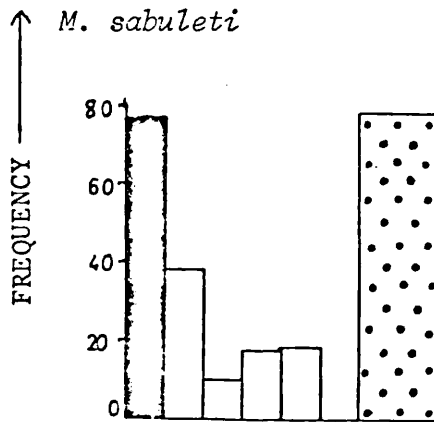
*M. scabrinodis*



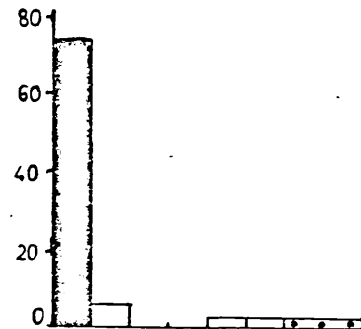
*M. ruginodis*



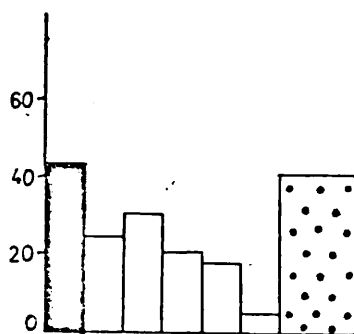
*M. sabuleti*



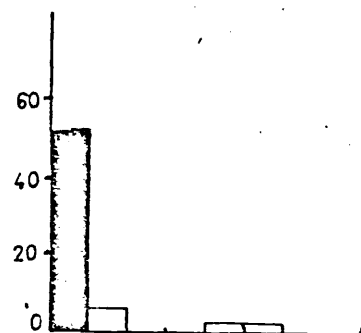
*M. rubra*



*M. shencki*



*M. sulcinodis*



KEY



Behaviour terminated within 2 seconds.  
 Behaviour sustained in ascending 3 second intervals.  
 Sustainment of all behaviour over 18 seconds.

SUSTAINMENT PERIOD →

FIGURE 30. Sustainment of the STILL response after a meeting with *L. flavus* by 6 *Myrmica* species in pair encounters.



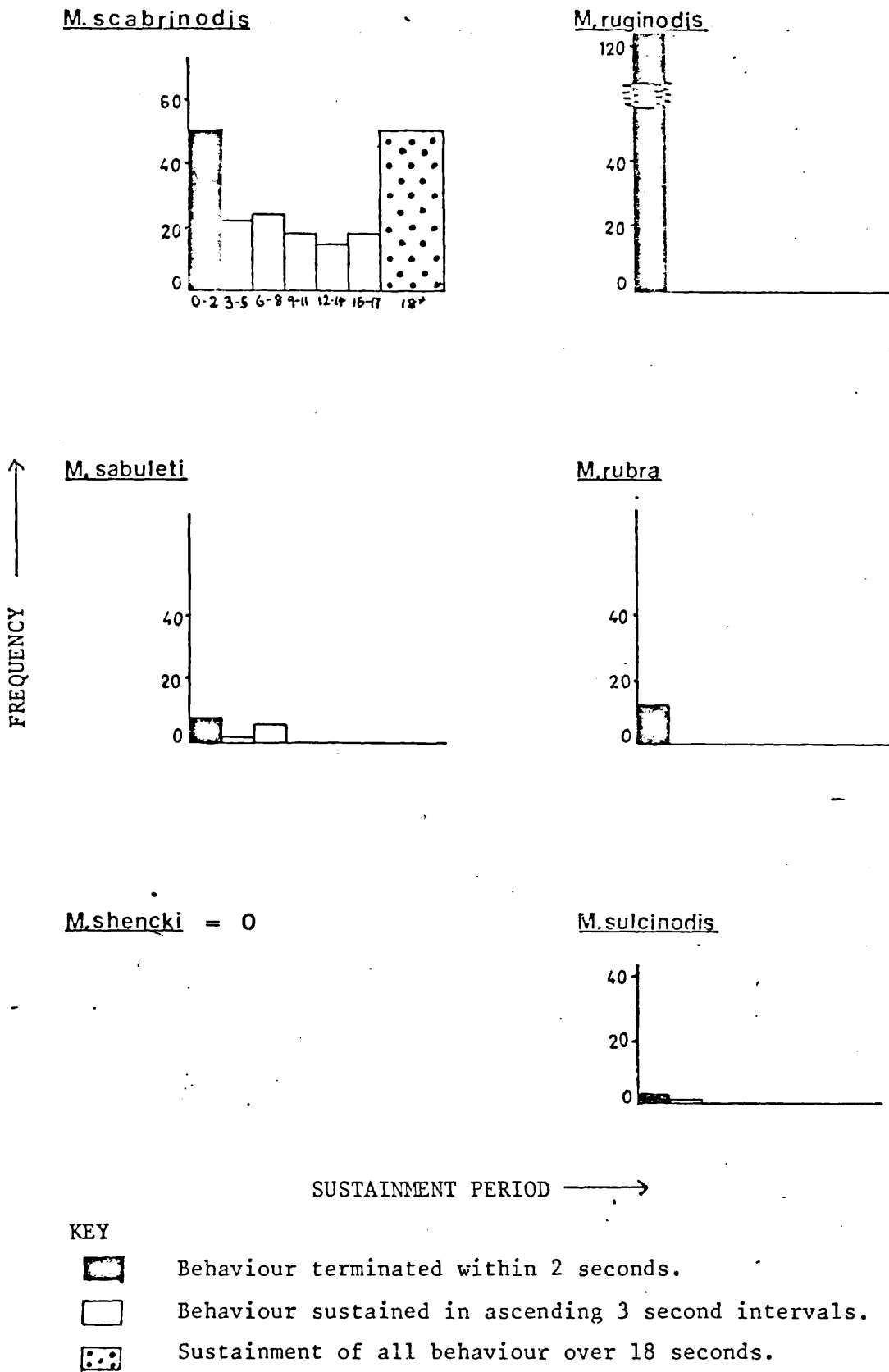


FIGURE 31. Sustainment of the ABDOMEN CURLING response after a meeting with *L. flavus* by 6 *Myrmica* species in pair encounters.

aggression was sometimes displayed. The *Lasius* was frequently threatened. CONFLICT was also shown but to a lesser extent. Fierce fighting frequently took place, at the first meeting. All the aggressive acts were performed a great deal. Dragging and stinging were particularly noticeable. The *Lasius* were killed and dismembered in several encounters. The *Myrmica* showed signs of injury and fled, particularly after having been 'drenched' by the enemy's abdominal secretions. Grooming bouts, by both opponents, were for long periods and took place after fierce interactions. 8 *Lasius* but no *Myrmica* were dead after 24 hours.

2.1.6. The behaviour of *L. flavus* towards 6 *Myrmica* species.

Some of the behavioural responses of the *Lasius* were similar to all 6 species of *Myrmica*. The ant approached each one showing threatening behaviour and a willingness to fight. It examined its opponents showing fast antennal activity and THREAT was often maintained for long periods. Further behaviour was also similar towards *M. scabrinodis*, *M. sabuleti* and *M. shencki*. The *Lasius* attacked the ants by biting, seizing and pulling actions. These attacks were not considered to be fierce - seizing and dragging were not prolonged and the gaster was rarely used.

The behaviour of the *Lasius* towards *M. ruginodis* was similar to that shown towards the previous 3 species. However, on occasions attacks were fiercer and gasters were employed.

The *Lasius* approached and attacked *M. rubra* and *M. sulcinodis* fiercely in many interactions. Fighting often began at the first meeting. Both of these species were bitten, seized and dragged strongly and often. The gaster was frequently used. Liquid from the *Lasius* gaster was clearly visible on the floor of the arena at times.

2.2. Comparison of Interactions.

Tables 49-63 compare the behavioural response of 6 *Myrmica* species in encounters with the same species of opponent, *L. flavus*, using 3 measurements of behaviour. The species are analysed in pairs and the following Key (Table 48) indicates the number of the Table in which each comparison is made.

Table 48. Key to Tables 49-63. The Key indicates the number of the Table in which each pair of *Myrmica* species are compared.

	<i>M. sabuleti</i>	<i>M. shencki</i>	<i>M. ruginodis</i>	<i>M. rubra</i>	<i>M. sulcinodis</i>
<i>M. scabrinodis</i>	49	50	55	58	61
<i>M. sabuleti</i>		51	56	59	62
<i>M. shencki</i>			57	60	63
<i>M. ruginodis</i>				53	54
<i>M. rubra</i>					52

It was convenient to arrange the species into 2 groups when analysing them\*

Group 1 : *M. scabrinodis*, *M. sabuleti* and *M. shencki*.

Group 2 : *M. ruginodis*, *M. rubra* and *M. sulcinodis*.

The species were then considered in the following order:-

- 1) Comparison of the 3 species in group 1 with each other (Tables 49-51).
- 2) Comparison of the 3 species of group 2 with each other (Tables 52-54).
- 3) Comparison of *M. ruginodis* with each of the species of group 1 (Tables 55-57)
- 4) Comparison of *M. rubra* with each of the species of group 1 (Tables 58-60).
- 5) Comparison of *M. sulcinodis* with each of the species of group 1 (Tables 61-63)

2.2.1 Comparison of *M. scabrinodis*, *M. sabuleti* and *M. shencki* with each other.

It was thought from observations that the 3 species behaved in a

---

\*The arrangement of species into these 2 groups does not affect their treatment but merely organises the order in which they are considered.

TABLE 49. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH *M. sabuleti* vs. *L. flavus*  
 (test animal) (opponent) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	16.5	**	1	18.5	**	1	n.a.	-	-
AVOID	45.0	N.S.	-	32.5	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	36.5	N.S.	-	33.0	N.S.	-
THREAT	36.0	N.S.	-	45.5	N.S.	-	46.0	N.S.	-
CONFLICT	38.0	N.S.	-	28.5	N.S.	-	35.0	N.S.	-
LUNGE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
BITE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
SEIZE	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
DRAG	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
STING	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
CHASE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
FLEE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
GROOM	30.0	N.S.	-	33.5	N.S.	-	33.0	N.S.	-
LOCOMOTION	38.0	N.S.	-	36.5	N.S.	-	25.0	N.S.	-
STILL	49.0	N.S.	-	6.0	***	2	0.0	***	2
ABDOMEN CURLING	12.0	**	1	6.5	***	1	0.0	***	1

TABLE 50 Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH

*M. shencki* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	30.0	N.S.	-	33.0	N.S.	-	n.a.	-	-
AVOID	43.0	N.S.	-	27.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	28.5	N.S.	-	42.0	N.S.	-
THREAT	30.0	N.S.	-	39.0	N.S.	-	39.0	N.S.	-
CONFLICT	33.0	N.S.	-	26.0	N.S.	-	32.5	N.S.	-
LUNGE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
BITE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
SEIZE	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
DRAG	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
STING	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
CHASE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
FLEE	30.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
GROOM	30.0	N.S.	-	26.5	N.S.	-	30.5	N.S.	-
LOCOMOTION	22.0	*	2	44.0	N.S.	-	26.0	N.S.	-
STILL	47.5	N.S.	-	7.5	***	2	0.0	***	2
ABDOMEN CURLING	1.0	***	1	0.0	***	1	0.0	***	1

TABLE 51. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. sabuleti* vs. *L. flavus*

COMPARED WITH

*M. shencki* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	41.0	N.S.	-	7.0	***	2	n.a.	-	-
AVOID	47.0	N.S.	-	39.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	36.0	N.S.	-	26.0	N.S.	-
THREAT	45.0	N.S.	-	49.5	N.S.	-	49.0	N.S.	-
CONFLICT	45.0	N.S.	-	46.0	N.S.	-	47.0	N.S.	-
LUNCE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
BITE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
SEIZE	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
DRAG	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
STING	50.0	N.S.	-	50.0	N.S.	-	50.0	N.S.	-
CHASE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
FLEE	30.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
GROOM	43.5	N.S.	-	37.5	N.S.	-	41.0	N.S.	-
LOCOMOTION	18.0	**	2	39.5	N.S.	-	43.0	N.S.	-
STILL	45.0	N.S.	-	37.5	N.S.	-	34.0	N.S.	-
ABDOMEN CURLING	28.0	N.S.	-	31.5	N.S.	-	34.0	N.S.	-

very similar way to each other when in encounters with *L. flavus*. The ants usually performed and sustained one of the 2 passive postures and never fought with the opponent. Statistical analysis (Tables 49-51) shows that few significant differences between the species are present. *M. scabrinodis* can be distinguished from the other 2 species by the greater amount of ABDOMEN-CURLING and correspondingly lesser amount of STILL behaviour it performed. *M. sabuleti* approaches the opponent more than the other 2 species. *M. shencki* shows LOCOMOTION sooner than the other 2 species. No other differences in the behaviour are detectable. The 2 species *M. sabuleti* and *M. shencki* (Table 51) are the most similar; indeed their behaviour towards the *Lasius* is almost identical.

#### 2.2.2 Comparison of *M. ruginodis*, *M. rubra* and *M. sulcinodis* with each other.

The behaviour of these three *Myrmica* species towards *L. flavus* is compared in Tables 52-54. It can be seen from Table 52 that few differences occur between *M. rubra* and *M. sulcinodis*. Both species were the only ones to fight fiercely and often with the *Lasius*. The latter did show biting, seizing and chasing more often than the former but no differences in duration can be found. *M. rubra* performed LOCOMOTION and THREAT sooner than *M. sulcinodis*.

*M. sulcinodis* was the only species to perform the 'ABDOMEN-CURLING-IN-LOCOMOTION' response (except for *M. ruginodis* which did it to a very slight extent) and this act is therefore a diagnostic feature of the ant.

The behaviour of *M. ruginodis* is compared with the behaviour of *M. rubra* and *M. sulcinodis* in Tables 53 and 54. Although *M. ruginodis* attacked and killed the *Lasius* in some cases, its behaviour was, generally, very different from that of the other 2 species. THREAT, CONFLICT, and SEIZE were shown far less by *M. ruginodis* than by the other 2 species

TABLE 52. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. rubra* vs. *L. flavus*.

COMPARED WITH *M. sulcinodis* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	49.5	N.S.	-	33.0	N.S.	-	n.a.	-	-
AVOID	23.5	N.S.	-	33.5	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	49.5	N.S.	-	50.0	N.S.	-
THREAT	11.5	**	1	34.5	N.S.	-	45.0	N.S.	-
CONFLICT	30.0	N.S.	-	32.5	N.S.	-	25.0	N.S.	-
LUNGE	42.0	N.S.	-	30.5	N.S.	-	n.a.	-	-
BITE	42.0	N.S.	-	15.0	**	2	n.a.	-	-
SEIZE	44.0	N.S.	-	22.0	*	2	25.0	N.S.	-
DRAG	47.5	N.S.	-	28.5	N.S.	-	25.5	N.S.	-
STING	44.0	N.S.	-	42.0	N.S.	-	32.0	N.S.	-
CHASE	44.5	N.S.	-	20.0	*	2	n.a.	-	-
FLEE	45.5	N.S.	-	47.5	N.S.	-	n.a.	-	-
GROOM	39.5	N.S.	-	32.5	N.S.	-	32.5	N.S.	-
LOCOMOTION	22.5	*	1	46.5	N.S.	-	33.5	N.S.	-
STILL	38.5	N.S.	-	38.5	N.S.	-	49.5	N.S.	-
ABDOMEN CURLING	33.5	N.S.	-	35.0	N.S.	-	40.5	N.S.	-
ABC. LOCOM	15.0	**	2	15.0	**	2	15.0	**	2



TABLE 53. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. ruginodis* vs. *L. flavus*

COMPARED WITH

*M. rubra* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	41.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
AVOID	42.0	N.S.	-	34.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	22.5	*	1	39.0	N.S.	-
THREAT	11.5	**	2	7.5	***	2	6.0	***	2
CONFLICT	5.5	***	2	19.0	**	2	21.5	*	2
LUNGE	33.0	N.S.	-	37.0	N.S.	-	n.a.	-	-
BITE	42.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
SEIZE	16.5	**	2	22.5	*	2	23.5	N.S.	-
DRAG	27.5	N.S.	-	31.5	N.S.	-	32.5	N.S.	-
STING	22.0	*	2	35.0	N.S.	-	34.0	N.S.	-
CHASE	41.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
FLEE	48.0	N.S.	-	39.0	N.S.	-	n.a.	-	-
GROOM	12.0	**	1	0.0	***	1	0.0	***	1
LOCOMOTION	46.0	N.S.	-	12.5	**	1	12.5	**	1
STILL	0.0	***	1	20.0	*	1	36.0	N.S.	-
ABDOMEN CURLING	29.5	N.S.	-	4.5	***	1	1.0	***	1

TABLE 54. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. ruginodis* vs. *L. flavus*  
(test animal) (opponent)

COMPARED WITH *M. sulcinodis* vs. *L. flavus*  
(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	40.0	N.S.	-	34.0	N.S.	-	n.a.	-	-
AVOID	25.0	N.S.	-	48.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	8.0	***	1	42.0	N.S.	-
THREAT	27.0	N.S.	-	4.0	***	2	7.0	***	2
CONFLICT	13.0	**	2	11.5	**	2	11.0	**	2
LUNGE	38.5	N.S.	-	25.0	N.S.	-	n.a.	-	-
BITE	49.0	N.S.	-	19.5	*	2	n.a.	-	-
SEIZE	7.5	***	2	15.0	**	2	17.0	**	2
DRAG	18.5	**	2	20.5	*	2	20.5	*	2
STING	23.0	*	2	29.5	N.S.	-	22.0	*	2
CHASE	31.5	N.S.	-	29.5	N.S.	-	n.a.	-	-
FLEE	46.0	N.S.	-	39.5	N.S.	-	n.a.	-	-
GROOM	21.0	*	1	29.5	N.S.	-	41.0	N.S.	-
LOCOMOTION	20.0	*	1	2.0	***	1	31.0	N.S.	-
STILL	40.0	N.S.	-	0.0	***	1	11.0	**	1
ABDOMEN CURLING	24.0	N.S.	-	0.0	***	1	2.0	***	1
ABC. LOCOM.	15.0	**	2	15.0	**	2	15.0	**	2

for almost every measurement employed. The ant also bit, dragged and stung the opponent less than did *M. sulcinodis*. *M. ruginodis* performed the passive responses, instead of fighting, in most meetings. STILL, ABDOMEN-CURLING, GROOM, LOCOMOTION and MEET are all done significantly more by *M. ruginodis* than by the other 2 *Myrmica*.

2.2.3 Comparison of *M. ruginodis* with *M. scabrinodis*, *M. sabuleti* and *M. shencki*.

The behaviour of *M. ruginodis* is compared with that of *M. scabrinodis*, *M. sabuleti* and *M. shencki* in Tables 55, 56 and 57 respectively. *M. ruginodis* differs in a similar way in its behaviour from each of the 3 species. Many differences between the species are present. *M. ruginodis* is more active in GROOM, LOCOMOTION and ABDOMEN-CURLING than are both *M. sabuleti* and *M. shencki*. The ant also performs the STILL response more often but for less time than these 2 species. *M. ruginodis* shows STILL and LOCOMOTION more than *M. scabrinodis* but ABDOMEN-CURLING is done to a lesser extent.

Some other differences are present. *M. ruginodis* shows AVOID sooner than does *M. sabuleti*, and sooner and more often than does *M. shencki*. It shows APPROACH less often than *M. scabrinodis*. Meetings are of longer duration than are ones with *M. scabrinodis* or *M. sabuleti* and less often than with *M. shencki*.

2.2.4. Comparison of *M. rubra* with *M. scabrinodis*, *M. sabuleti* and *M. shencki*.

The behaviour of *M. rubra* with that of *M. scabrinodis*, *M. sabuleti* and *M. shencki* is compared in Tables 58, 59 and 60 respectively. The behaviour of *M. rubra* is very different from that of the other 3 species. *M. rubra* threatens and seizes the opponent more for each of the measurements employed. CONFLICT is shown sooner, and AVOID both sooner and

TABLE 55. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH *M. ruginodis* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	33.5	N.S.	-	17.0	**	1	n.a.	-	-
AVOID	24.0	N.S.	-	48.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	36.0	N.S.	-	23.0	*	2
THREAT	48.5	N.S.	-	49.0	N.S.	-	49.5	N.S.	-
CONFLICT	24.0	N.S.	-	18.0	**	1	17.5	**	1
LUNGE	45.0	N.S.	-	45.0	N.S.	-	n.a.	-	-
BITE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
SEIZE	45.0	N.S.	-	45.0	N.S.	-	45.0	N.S.	-
DRAG	45.0	N.S.	-	45.0	N.S.	-	45.0	N.S.	-
STING	45.0	N.S.	-	45.0	N.S.	-	45.0	N.S.	-
CHASE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
FLEE	30.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
GROOM	13.5	**	2	25.0	N.S.	-	26.5	N.S.	-
LOCOMOTION	5.0	***	2	1.5	***	2	8.0	***	2
STILL	40.0	N.S.	-	0.0	***	2	16.0	**	2
ABDOMEN CURLING	35.0	N.S.	-	14.5	**	1	3.0	***	1

TABLE 56. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. sabuleti* vs. *L. flavus*  
(test animal) (opponent)

COMPARED WITH *M. ruginodis* vs. *L. flavus*  
(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	45.5	N.S.	-	46.0	N.S.	-	n.a.	-	-
AVOID	17.0	**	2	28.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	29.0	N.S.	-	16.0	**	2
THREAT	40.5	N.S.	-	38.5	N.S.	-	38.5	N.S.	-
CONFLICT	35.0	N.S.	-	34.5	N.S.	-	32.5	N.S.	-
LUNGE	45.0	N.S.	-	45.0	N.S.	-	n.a.	-	-
BITE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
SEIZE	45.0	N.S.	-	45.0	N.S.	-	45.0	N.S.	-
DRAG	45.0	N.S.	-	45.0	N.S.	-	45.0	N.S.	-
STING	45.0	N.S.	-	45.0	N.S.	-	45.0	N.S.	-
CHASE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
FLEE	30.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
GROOM	6.0	***	2	5.5	***	2	4.0	***	2
LOCOMOTION	12.0	**	2	10.5	**	2	21.0	*	2
STILL	31.5	N.S.	-	10.0	***	2	3.0	***	1
ABDOMEN CURLING	19.0	**	2	0.0	***	2	8.0	***	2

TABLE 57. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. shencki* vs. *L. flavus*

COMPARED WITH

*M. ruginodis* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	50.0	N.S.	-	41.5	N.S.	-	n.a.	-	-
AVOID	17.0	**	2	23.0	*	2	n.a.	-	-
MEET	n.a.	-	-	19.5	*	2	37.0	N.S.	-
THREAT	38.5	N.S.	-	38.5	N.S.	-	38.5	N.S.	-
CONFLICT	39.5	N.S.	-	39.5	N.S.	-	38.5	N.S.	-
LUNGE	45.0	N.S.	-	45.0	N.S.	-	n.a.	-	-
BITE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
SEIZE	45.0	N.S.	-	45.0	N.S.	-	45.0	N.S.	-
DRAG	45.0	N.S.	-	45.0	N.S.	-	45.0	N.S.	-
STING	45.0	N.S.	-	45.0	N.S.	-	45.0	N.S.	-
CHASE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
FLEE	44.0	N.S.	-	44.0	N.S.	-	n.a.	-	-
GROOM	9.0	***	2	1.0	***	2	9.0	***	2
LOCOMOTION	47.0	N.S.	-	0.0	***	2	13.0	**	2
STILL	33.5	N.S.	-	0.0	***	2	1.0	***	1
ABDOMEN CURLING	0.0	***	2	0.0	***	2	0.0	***	2

TABLE 58. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH *M. rubra* vs. *L. flavus*.

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	44.0	N.S.	-	18.5	**	1	n.a.	-	-
AVOID	25.0	N.S.	-	34.5	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	28.0	N.S.	-	36.5	N.S.	-
THREAT	8.0	***	2	5.0	***	2	6.0	***	2
CONFLICT	30.5	N.S.	-	35.0	N.S.	-	30.5	N.S.	-
LUNGE	30.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
BITE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
SEIZE	15.0	**	2	15.0	**	2	15.0	**	2
DRAG	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
STING	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
CHASE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
FLEE	25.0	N.S.	-	25.0	N.S.	-	n.a.	-	-
GROOM	28.0	N.S.	-	26.0	N.S.	-	34.5	N.S.	-
LOCOMOTION	12.5	**	2	47.0	N.S.	-	47.0	N.S.	-
STILL	41.5	N.S.	-	31.0	N.S.	-	42.0	N.S.	-
ABDOMEN CURLING	27.0	N.S.	-	16.0	**	1	0.0	***	1

TABLE 59. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1. GROUP 2.  
*M. sabuleti* vs. *L. flavus* COMPARED WITH *M. rubra* vs. *L. flavus*  
 (test animal) (opponent) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	30.0	N.S.	-	46.5	N.S.	-	n.a.	-	-
AVOID	14.0	**	2	20.5	*	2	n.a.	-	-
MEET	n.a.	-	-	31.5	N.S.	-	29.5	N.S.	-
THREAT	3.0	***	2	0.0	***	2	0.5	***	2
CONFLICT	18.0	**	2	36.0	N.S.	-	37.0	N.S.	-
LUNGE	30.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
BITE	50.0	N.S.	-	50.0	N.S.	-	n.a.	-	-
SEIZE	15.0	**	2	15.0	**	2	15.0	**	2
DRAG	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
STING	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
CHASE	35.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
FLEE	25.0	N.S.	-	25.0	N.S.	-	n.a.	-	-
GROOM	43.5	N.S.	-	35.0	N.S.	-	35.5	N.S.	-
LOCOMOTION	18.0	**	2	44.0	N.S.	-	31.0	N.S.	-
STILL	45.0	N.S.	-	42.0	N.S.	-	7.0	***	1
ABDOMEN CURLING	22.5	*	2	28.5	N.S.	-	43.0	N.S.	-



TABLE 60. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. shencki* vs. *L. flavus*

COMPARED WITH

*M. rubra* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	39.5	N.S.	-	41.5	N.S.	-	n.a.	-	-
AVOID	17.0	**	2	16.5	**	2	n.a.	-	-
MEET	n.a.	-	-	36.0	N.S.	-	49.0	N.S.	-
THREAT	0.5	***	2	0.0	***	2	0.0	***	2
CONFLICT	10.5	**	2	33.5	N.S.	-	38.5	N.S.	-
LUNGE	30.0	N.S.	-	30.0	N.S.	-	n.a.	-	-
BITE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
SEIZE	15.0	**	2	15.0	**	2	15.0	**	2
DRAG	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
STING	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
CHASE	40.0	N.S.	-	40.0	N.S.	-	n.a.	-	-
FLEE	44.0	N.S.	-	44.0	N.S.	-	n.a.	-	-
GROOM	49.5	N.S.	-	48.5	N.S.	-	47.0	N.S.	-
LOCOMOTION	49.5	N.S.	-	49.5	N.S.	-	37.0	N.S.	-
STILL	46.0	N.S.	-	49.0	N.S.	-	2.0	***	1
ABDOMEN CURLING	0.0	***	2	13.0	**	2	16.5	**	2

more often by *M. rubra* than by *M. shencki*. *M. rubra* performed the STILL posture in some interactions; however, this posture was performed for far longer by *M. sabuleti* and *M. shencki*. Similarly *M. rubra* performed some ABDOMEN-CURLING but this was done far more by *M. scabrinodis*.

2.2.5. Comparison of *M. sulcinodis* with *M. scabrinodis*, *M. sabuleti* and *M. shencki*.

The behaviour of *M. sulcinodis* is compared with *M. scabrinodis*, *M. sabuleti* and *M. shencki* in Tables 61, 62 and 63 respectively. *M. sulcinodis* was believed to be the most aggressive ant of the 6 *Myrmica* species tested. The ant shows more THREAT, LUNGE, BITE, SEIZE, DRAG and CHASE than the other 3 species for most of the measurements tested. *M. sulcinodis* fled more than did *M. scabrinodis* and *M. sabuleti* but not more than did *M. shencki*. *M. sulcinodis* was engaged in combat for long periods. Meetings occurred more often with *M. scabrinodis*, and more often and for longer with *M. sabuleti*. *M. sulcinodis* performed the passive acts less than the other 3 species. Both *M. sabuleti* and *M. shencki* are STILL more and for longer. ABDOMEN-CURLING is done more, for longer and sooner by *M. scabrinodis* and *M. sabuleti*.

2.2.6. Comparison of the total number of significant differences in the responses of the 6 *Myrmica* species.

It was thought convenient to summarise the differences found between the *Myrmica* species in Tables 49-63. The significant differences 1) for all responses and 2) for the 4 aggressive acts (T.S.D. St.) for all 3 measurements that resulted from each comparison were summed (i.e. the total number of significant differences that occurred in each of Tables 49-63). These totals are shown in Table 64.

TABLE 61. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. scabrinodis* vs. *L. flavus* COMPARED WITH *M. sulcinodis* vs. *L. flavus*  
 (test animal) (opponent) (test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	48.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
AVOID	41.0	N.S.	-	48.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	12.0	**	1	40.0	N.S.	-
THREAT	17.0	**	2	2.5	***	2	3.0	***	2
CONFLICT	41.0	N.S.	-	49.0	N.S.	-	46.0	N.S.	-
LUNGE	15.0	**	2	15.0	**	2	n.a.	-	-
BITE	15.0	**	2	15.0	**	2	n.a.	-	-
SEIZE	10.0	***	2	10.0	***	2	10.0	***	2
DRAG	15.0	**	2	15.0	**	2	15.0	**	2
STING	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
CHASE	20.0	*	2	20.0	*	2	n.a.	-	-
FLEE	20.0	*	2	20.0	*	2	n.a.	-	-
GROOM	46.0	N.S.	-	49.0	N.S.	-	45.0	N.S.	-
LOCOMOTION	28.0	N.S.	-	41.0	N.S.	-	34.0	N.S.	-
STILL	46.0	N.S.	-	35.0	N.S.	-	46.0	N.S.	-
ABDOMEN CURLING	17.5	**	1	2.0	***	1	0.0	***	1
ABC LOCOM.	15.0	**	2	15.0	**	2	15.0	**	2

TABLE 62. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. sabuleti* vs. *L. flavus*

COMPARED WITH

*M. sulcinodis* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	29.0	N.S.	-	36.0	N.S.	-	n.a.	-	-
AVOID	34.0	N.S.	-	35.0	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	22.0	*	1	16.0	**	2
THREAT	9.0	***	2	0.0	***	2	0.0	***	2
CONFLICT	30.0	N.S.	-	25.0	N.S.	-	35.0	N.S.	-
LUNGE	20.0	*	2	20.0	*	2	n.a.	-	-
BITE	15.0	**	2	15.0	**	2	n.a.	-	-
SEIZE	10.0	***	2	10.0	***	2	10.0	***	2
DRAG	15.0	**	2	15.0	**	2	15.0	**	2
STING	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
CHASE	20.0	*	2	20.0	*	2	n.a.	-	-
FLEE	30.0	N.S.	-	20.0	*	2	n.a.	-	-
GROOM	40.5	N.S.	-	38.5	N.S.	-	4.0	***	2
LOCOMOTION	26.5	N.S.	-	49.5	N.S.	-	21.0	*	2
STILL	46.5	N.S.	-	14.5	**	1	3.0	***	1
ABDOMEN CURLING	39.5	N.S.	-	40.5	N.S.	-	8.0	***	1

TABLE 63. Comparison of the responses of test animals in 2 groups of experimental encounter, using 3 measurements of behaviour. The table shows the Mann-Whitney statistic (U) and the associated probability level (P) and indicates the group (G) having the higher score (see page 26 for key).

GROUP 1.

GROUP 2.

*M. shencki* vs. *L. flavus*

COMPARED WITH *M. sulcinodis* vs. *L. flavus*

(test animal) (opponent)

(test animal) (opponent)

BEHAVIOURAL RESPONSE	LATENCY			OCCURRENCE			DURATION		
	U	P	G	U	P	G	U	P	G
APPROACH	31.0	N.S.	-	44.0	N.S.	-	n.a.	-	-
AVOID	35.0	N.S.	-	28.5	N.S.	-	n.a.	-	-
MEET	n.a.	-	-	28.0	N.S.	-	47.0	N.S.	-
THREAT	0.0	***	2	0.0	***	2	0.0	***	2
CONFLICT	22.0	*	2	26.0	N.S.	-	28.0	N.S.	-
LUNGE	15.0	**	2	15.0	**	2	n.a.	-	-
BITE	15.0	**	2	15.0	**	2	n.a.	-	-
SEIZE	10.0	***	2	10.0	***	2	10.0	***	2
DRAG	15.0	**	2	15.0	**	2	15.0	**	2
STING	25.0	N.S.	-	25.0	N.S.	-	25.0	N.S.	-
CHASE	20.0	*	2	20.0	*	2	n.a.	-	-
FLEE	46.0	N.S.	-	46.0	N.S.	-	n.a.	-	-
GROOM	39.5	N.S.	-	32.5	N.S.	-	34.0	N.S.	-
LOCOMOTION	33.5	N.S.	-	38.0	N.S.	-	42.5	N.S.	-
STILL	44.0	N.S.	-	15.0	**	1	0.0	***	1
ABDOMEN CURLING	14.0	**	2	24.0	N.S.	-	30.0	N.S.	-
ABC. LOCOM.	15.0	**	2	15.0	**	2	15.0	**	2

Table 64. Total numbers of differences in responses, for 3 measurements of behaviour, between pairs of *Myrmica* species in experimental encounters with *L. flavus*.

<i>Myrmica</i> species compared.	Total number of significant differences for all responses.	Total number of significant differences for the 4 aggressive acts THREAT, SEIZE, DRAG, STING.
<i>M. sabuleti</i> with <i>M. shencki</i>	2	0
<i>M. scabrinodis</i> with <i>M. shencki</i>	6	0
<i>M. scabrinodis</i> with <i>M. sabuleti</i>	7	0
<i>M. sulcinodis</i> with <i>M. rubra</i>	8	2
<i>M. ruginodis</i> with <i>M. rubra</i>	19	6
<i>M. ruginodis</i> with <i>M. sulcinodis</i>	25	9
<i>M. ruginodis</i> with <i>M. scabrinodis</i>	12	0
<i>M. ruginodis</i> with <i>M. sabuleti</i>	13	0
<i>M. ruginodis</i> with <i>M. shencki</i>	13	0
<i>M. rubra</i> with <i>M. scabrinodis</i>	10	6
<i>M. rubra</i> with <i>M. sabuleti</i>	12	6
<i>M. rubra</i> with <i>M. shencki</i>	13	6
<i>M. sulcinodis</i> with <i>M. scabrinodis</i>	20	9
<i>M. sulcinodis</i> with <i>M. sabuleti</i>	27	9
<i>M. sulcinodis</i> with <i>M. shencki</i>	21	9

It can be seen from Table 64 that the fewest number of differences for all responses occur between *M. scabrinodis*, *M. sabuleti* and *M. shencki*. *M. rubra* and *M. sulcinodis* are also very similar. Both of them are very different from *M. ruginodis*. Both *M. rubra* and *M. ruginodis* show

a similar number of differences from the 3 species of group 1 (*M. scabrinodis*, *M. sabuleti* and *M. shencki*). However it can be seen from Tables 55-60 that these differences occur with respect to different responses in each case. Total number of differences in behaviour cannot therefore be used as an absolute guide to the closeness of species. By far the largest number of differences occur between *M. sulcinodis* and other ants (with the exception of *M. rubra*).

When only the aggressive acts are examined it can be seen that *M. ruginodis* shows no significant differences from *M. scabrinodis*, *M. sabuleti* and *M. shencki*. *M. rubra* differs from these 3 species in 6 measurements and *M. sulcinodis* shows the greatest number of differences (9).

### 2.3. Comparison of the STILL and ABDOMEN-CURLING responses.

#### 1) Occurrence and Duration.

The two responses were shown to some extent by all the species. The scores for these acts for occurrence and duration have already been compared in Tables 49-63 above.

#### 2) Sustainment behaviour.

Sustainment of the STILL and ABDOMEN-CURLING postures after a meeting by the 6 *Myrmica* species is shown in Figures 30 and 31, respectively. The behaviour has been described for each of the species separately in 2.1. above. The species are briefly compared with respect to this behaviour here.

##### a) The STILL response.

It can be seen from Figure 30 that *M. scabrinodis*, *M. sabuleti* and *M. shencki* are similar in that they all sustain the posture for long periods after a meeting. The remaining 3 species, *M. ruginodis*, *M. rubra* and *M. sulcinodis*, in contrast do not. These species terminate the posture within a second or so after a meeting and begin LOCOMOTION.

b) The ABDOMEN-CURLING response.

ABDOMEN-CURLING is performed often by only 2 species, *M. scabrinodis* and *M. ruginodis*. Figure 31 shows how the behaviour is frequently sustained for very long periods after a meeting by *M. scabrinodis* but terminated immediately by *M. ruginodis*. *M. ruginodis* usually began LOCOMOTION immediately. It should be noted that *M. ruginodis* only curled its abdomen when touched there by the opponent whereas *M. scabrinodis* did so even when other parts of its body were stimulated.

3) The 'Form' of the STILL posture.

Various forms of the STILL posture were exhibited by the 6 *Myrmica* species. The differences were most apparent in the position of the antennae and height of the body. Figure 32 summarises these differences and indicates the species that usually performed each type.

*M. scabrinodis* typically withdrew both its antennae simultaneously and tucked them in closely beside the head when examined or attacked by the opponent (Figure 32a). The response was made even when parts of the body other than the head region were touched. For example, if the opponent approached from the rear and touched the abdomen of the *Myrmica* the antennae were retracted. *M. sabuleti* also performed the behaviour in a similar way to *M. scabrinodis*. Both species adopted a low crouched posture (Figure 32e), compared with the higher postures of the other *Myrmica* (Figure 32f).

*M. shencki* sometimes withdrew both antennae simultaneously. Usually, however, the antennae remained extended. If one of them was then touched by the opponent it was withdrawn and tucked in beside the head. The other antenna, not stimulated, remained extended (Figure 32b). This behaviour was also shown to a lesser extent by *M. sabuleti* and *M. ruginodis*.



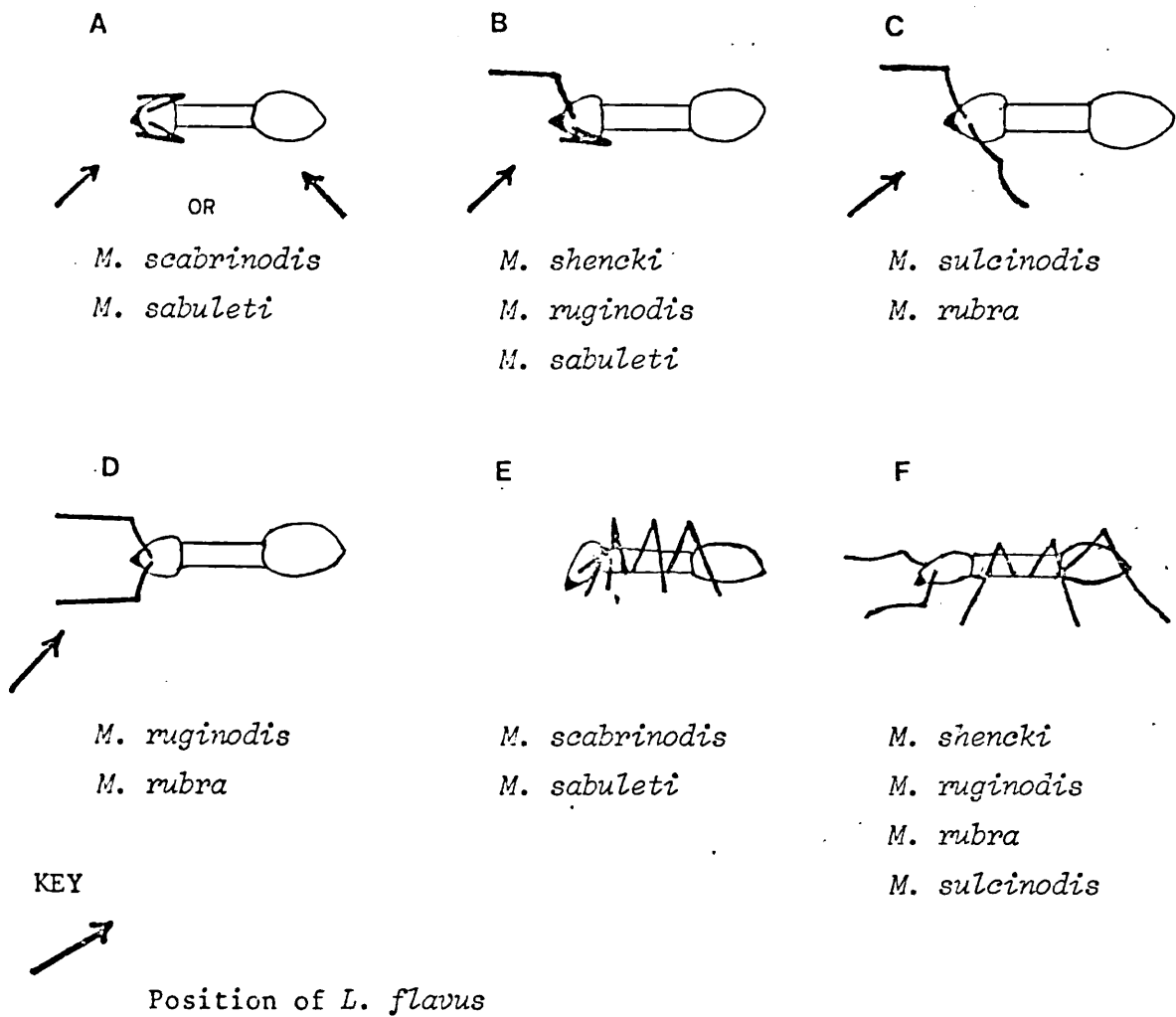


FIGURE 32. Form of the STILL response shown by 6 *Myrmica* species when attacked by *L. flavus*.

*M. ruginodis* maintained a high body position in its STILL posture and the head was not lowered. The antennae remained extended and they were often not moved when touched by the opponent (Figure 32d). If the opponent bit or vigorously examined the antennae they were then retracted but not maintained in that position for any length of time.

*M. sulcinodis* and *M. rubra* usually withdrew only 1 antenna away from the opponent when the antenna was touched. However, the antenna was held back away from the stimulus rather than tucked in (Figure 32c).

### 3. Discussion

It has been stated that the 6 *Myrmica* species studied in these experiments are very closely related. The species are sometimes separated into groups based on similarities in morphological characters. Bernard (1968), for example, recognises 2 basic groups by the antennal shape of males:-

GROUP 1 : *M. ruginodis*, *M. rubra*, *M. sulcinodis*, *M. lobicornis*.

GROUP 2 : *M. scabrinodis*, *M. sabuleti*, *M. shencki*.

Elmes (1975) discusses 3 groups determined by morphometric analysis of female characteristics:-

GROUP 1 : *M. scabrinodis*, *M. sabuleti*.

GROUP 2 : *M. rubra*, *M. ruginodis*.

GROUP 3 : *M. sulcinodis*, *M. lobicornis*.

Identification to the species level is usually determined by characters such as petiole, scape, epinotal spine, frons ratio, head width, body striations and colour.

The experiments of this study showed that the 6 species can also be distinguished from one another by a quantitative analysis of their behaviour. Furthermore, the species can be placed into 2 or 3 groups by their behavioural traits, as follows:-

GROUP 1 : *M. scabrinodis*, *M. sabuleti*, *M. shencki*.

GROUP 2 : *M. ruginodis*.

GROUP 3 : *M. rubra*, *M. sulcinodis*.

From this it would appear that behavioural differences are correlated to some extent with morphological ones. The ants *M. scabrinodis*, *M. sabuleti* and *M. shencki* of GROUP 1 behaved in a very similar way to one another and differently from the rest. In fact, the tactics employed by these 3 species towards an *L. flavus* opponent were similar in and throughout all encounters. They were characterised by slow and deliberate movement

and by a tendency to approach rather than avoid. Also, on meeting the opponent the ants became passive and sustained the motionless postures after the enemy had departed (the other 3 species rarely did this).

Fighting was not seen and mortalities did not occur.

All 3 species are morphologically similar and intermediate forms are found (Donisthorpe, 1927). *M. sabuleti* was once considered to be a variety of *M. scabrinodis*. The former is also found in the same nest as *L. flavus* but to a lesser degree and probably prefers a warmer habitat than the latter. It is not surprising then that the 2 species behave in a very similar way. *M. scabrinodis* could be distinguished from both *M. sabuleti* and *M. shencki*, however, by the much greater amount of ABDOMEN-CURLING that it performed. The importance of this behaviour to the ant's relationship with *L. flavus* has been discussed in Chapter 3. It would be interesting to know the behaviour of *M. sabuleti* and *M. shencki* in compound nests with *L. flavus*.

Few quantitative differences in behaviour could be detected between *M. sabuleti* and *M. shencki*.

The 3 species are different from the others in that the base of their scape is sharply bent. Brian (1956a) suggests that this may be adapted for movement by *M. scabrinodis* in dense vegetation, as the ant tends to forage close to the ground. It seems probable however that the structure permits the antennae to be closely folded into the body for protective reasons. The tactics of the 3 species rely on their ability to remain motionless when under attack. A more vulnerable antennal position would jeopardise this and may also be a stimulus increasing aggression in the opponent.

*M. ruginodis*, *M. rubra* and *M. sulcinodis* do not perform and sustain the passive behaviour in the same way as the species of GROUP 1 and their antennal scapes are more evenly curved. Their activity is

generally high and locomotion is at a much faster rate. *M. ruginodis* and *M. rubra* are believed to be closely related (Pickles, 1940). The distribution of *M. rubra* and *M. ruginodis* is given by Stradling (1968). Experiments from this study show that the behaviour of *M. rubra* and *M. sulcinodis* is similar and distinctly different from *M. ruginodis*. All 3 species show differing responses on meeting *L. flavus* (in contrast to GROUP 1 species) but only *M. rubra* and *M. sulcinodis* fight to any extent. Both species are predaceous and *M. sulcinodis* preys on other ants a great deal. It is interesting that while some *M. rubra* died as a result of combats, no deaths occurred in *M. sulcinodis*. *M. rubra* is sometimes found in the same nest mound as *L. flavus* but here it would seem to be competing for resources, as Elmes (1974) has shown that the 2 species are not associated.

*M. ruginodis* like *M. rubra* is segregated from *L. flavus* in the field (Pickles, 1940). Both these species are believed to be the most 'war-like' of the *Myrmica* and sting freely (Donisthorpe, 1913). *M. ruginodis* rarely attacks *L. flavus* in these experiments and indeed its passive behaviour is more like the species of GROUP 1 than those of GROUP 3 - although the actual STILL posture is quite different. When a *Myrmica* remains motionless in an encounter it is the *L. flavus* that determines the length of the meeting. Meetings were of longer durations with *M. ruginodis* than with either *M. scabrinodis* or *M. sabuleti*. This may reflect the effectiveness of a 'submissive' individual over merely a 'still' one (*M. shencki* also adopted a relatively 'high' posture). By morphometric analysis (Elmes, 1975) *M. sulcinodis* is suggested to be intermediate between the *M. rubra/ruginodis* group and the *M. scabrinodis/sabuleti* group. By a quantitative behavioural analysis the order of relationship (based on the number of significant differences

between the species) is as follows:

*M. sulcinodis* - *M. rubra* - *M. ruginodis* - *M. scabrinodis/sabuleti*  
*/shencki*.

Although the 6 *Myrmica* species are closely related they do have different optimal habitat and food preferences. Interspecific competition has produced the changes in physiology and behaviour to enable the species to utilize the different habitats and to survive in the presence of specific competitors. The experiments have shown that closely related species may employ different tactics even to one type of opponent in pair encounters. The behaviour of groups of animals to different opponents and in different conditions would undoubtedly reveal a variety of additional behaviour patterns.

Marikowski (1962) states that *F. rufa* will cause *M. rubra* and *L. niger* to lead a more subterranean existence. *F. lemni*, *M. scabrinodis* and *M. ruginodis* compete for a nest site in this descending order of success (Brian, 1958). The less successful colonies will have to take a less suitable nest site. Both examples further illustrate the ability of ants to modify their behaviour to suit a given situation. The findings here that taxonomically closely related species, such as *M. rubra* and *M. ruginodis*, may behave quite differently emphasises the need to consider the ecological positions of the species when investigating aggression and possible competition. Reference has already been made to pheromone analysis in *Myrmica* (see page 114).

*Myrmica* have been compared with respect to their pheromones by Crew and Blum (1970) and Cammaerts *et al*, (1978). By combining behavioural studies with taxonomic and pheromonal ones a more complete understanding of the relationship between species can be gained.

Most ants exhibit a degree of patterning in their activities. The different temporal foraging patterns of *Tapinoma antarcticum* and *Dorymyrmex antarcticus*, for example, enables a partitioning of resources

amongst the coexisting species (Hunt, 1974). Studies have been done on the patterning of a wider variety of acts in a given situation, for example, with the agonistic behaviour of great tits, *Parus major* (Blurton Jones, 1968) and the aggressive behaviour of the mantis shrimp *Gonodactylus bredini* (Dingle, 1969a, b). The temporal patterning of an act may be influenced by the occurrence of another. Sequential analysis has been much investigated (see Hinde and Stevenson, 1969; Slater, 1972). It has been discussed previously how animals when fighting cannot perform other responses. Acts may occur close together because of common causation, as in fighting.

Analysis of temporal patterning of responses has proved to be very useful for describing behaviour in these experiments. The analysis reflects the type of interaction taking place between 2 species. The behaviour of the 6 *Myrmica* species towards *L. flavus* is taken to illustrate this. Figure 33 shows the temporal patterning of the occurrence of all responses summed for each 5 minute period of the 30 minute encounter. It was seen that very little fighting occurred with *M. scabrinodis*, *M. sabuleti* and *M. shencki*. The uniform behaviour of these ants towards the opponent throughout the encounter is reflected here. In contrast, *M. ruginodis*, *M. rubra* and *M. sulcinodis* all fought with the *Lasius* to an extent. The graphs show the relatively greater activity of their overall behaviour. Furthermore, it can be seen that in encounters where fighting occurs, the interactions are most intense initially and that these decrease with time. This high initial activity in aggressive interactions was also seen in some individual acts such as THREAT, SEIZE, CHASE, etc. However, in some encounters some acts showed an increase with time. There seems to be no hard and fast rule as to which kind of response will show a change with time but rather that this depends on the type of encounter.

*M. ruginodis*

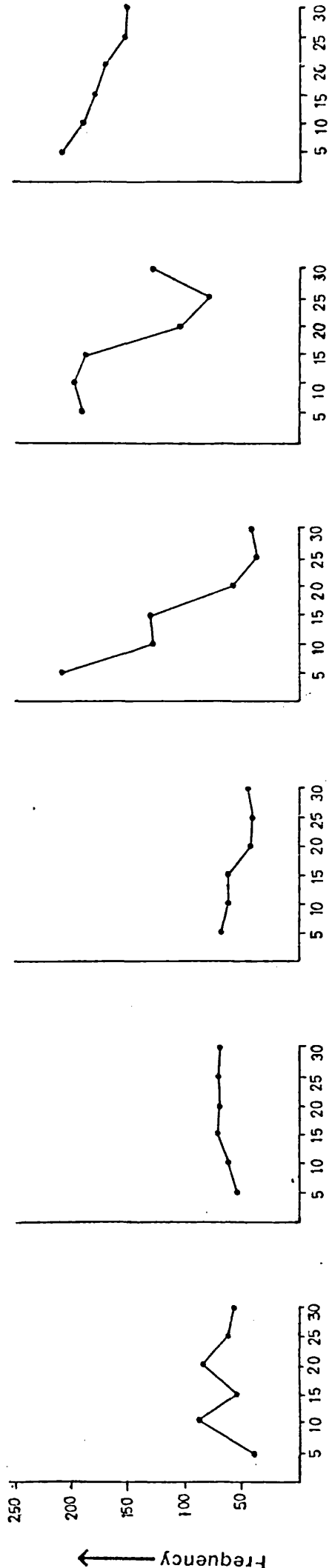
*M. sulcinodis*

*M. rubra*

*M. shencki*

*M. sabuleti*

*M. scabrinodis*



TIME (mins) →

FIGURE 33. Temporal patterning of the mean frequency of occurrence of all responses shown by 6 *Myrmica* species in 30 minute pair encounters with *L. flavus*. (n = 10)



CHAPTER 6

GENERAL DISCUSSION

## GENERAL DISCUSSION

By examining a large number of responses shown by individual ants in pair-encounter experiments and by measuring them in 3 different ways it has been possible to obtain a full and quantitative analysis of the complex process of interspecific aggressive behaviour. Such a study has also permitted a critical assessment of the various responses exhibited by the ants and of the measurements employed in their study. It has been stated that the 4 responses THREAT, SEIZE, DRAG and STING are felt necessary to record aggressive interactions in ants. Further, an examination of the 3 measurements occurrence, duration and latency has shown that the importance of each one varies depending on the type of interaction investigated. Both occurrence and duration of the responses are required, and the examples chosen to demonstrate this clearly show that there is a danger in basing a hypothesis of aggression on just one measurement.

The variability of behaviour was stated earlier (from Wilson 1971) to consist of 3 components, polymorphism, age polyethism and 'all remaining variation.' As the *Myrmica* species studied were relatively monomorphic so the influence of form on behaviour was neglected. Weir (1958) has recorded some aspects of age polyethism in *M. scabrinodis*. Several experiments here have also shown that the behaviour of both individuals and groups of *M. scabrinodis* is variable with age. Individuals show differences in exploratory activity, grooming behaviour and also in postural responses such as ABDOMEN-CURLING. It was the older animals in colony interactions that confronted *L. flavus* opponents and by their blocking and building activity succeeded in gaining nest territory and retaining nest identity.

The last of Wilson's categories, 'all remaining variation' would seem to be large even when only the aggressive aspects of ant behaviour

are considered. Experiments have shown the degree to which a number of factors will influence the aggressive behaviour of a given individual and of entire colonies. The relative colony sizes of the interacting species and the place of interaction were seen to be the most important factors affecting the motivation and willingness of the animals to fight. *M. scabrinodis* was more aggressive near its nest entrance and inside the nest than at distances away from it. The presence of both the queen and brood increase the aggressive responses of *M. scabrinodis* workers (Moxon, unpublished). However, such influencing factors are secondary to the relative number of interacting ants. When *M. scabrinodis* are attacked by a relatively large *L. flavus* force the former behave passively (after a brief period of initial encounters) at places where they were formerly aggressive, including inside their own nest. It is obviously disadvantageous for animals to remain and fight in an area when hopelessly outnumbered. Ants are known to be displaced from nest sites (Brian, 1952a; Scherba, 1964) and feeding areas (Talbot, 1943; De Vroey, 1978) by stronger competitors. The strength of the colony and also the motivation of its members to fight at a given place are reflected in the number of individuals recruited to and interacting at that place. Chapter 3 discussed a chemical mechanism by which the relative strength of 2 interacting colonies may be perceived by each side. Abnormally, small colonies of some species of ant, e.g. *Formica rufa*, cannot be cultured successfully in the laboratory, probably because of the inability of the ants to perform the tasks of the missing types of worker. It may well be that when differential mortality occurs in a battle the dead fighters are not replaced as their sisters are unwilling to assume a fighting role. The information of a temporal change in the relative number of individuals interacting, due to differential mortality or an increase in recruitment by one species may also be perceived by the same kind of chemical mechanism described in Chapter 3.

The experimental arena was found to be a suitable way to standardise the 'place of interaction' factor in comparative studies of aggressive behaviour. The main criticism of its use is that it does not permit escape or avoidance by the animals that might occur under natural circumstances. The aims of the experiments, however, were to compare the inherent behavioural responses of different species with each other and of the same species under different experimental conditions rather than to investigate the usual behaviour of individuals in the wild. Indeed, investigations have shown that the behaviour of a given type of ant is variable in different circumstances, and that there is no one or 'usual' way than an ant will behave. It may be felt by some authors that flight rather than fight is the rule when ants meet in the wild. However, many examples have been quoted in the text where combat does occur in the natural conditions. Animals will fight when there is a need to do so and when the probability of winning is high. Thus a solitary worker away from her nest and nest mates would be expected to avoid aggressive encounters. It was seen how the strategy of *L. niger* is rapid avoidance while *M. scabrinodis*, *M. sabuleti* and *M. shencki* become motionless. Both types of behaviour avoid combat. At the other extreme, a subterranean ant like *L. flavus* or *L. umbratus* is highly motivated to approach and attack aliens in its nest, for reasons discussed in Chapter 3.

The effectiveness of a species in combat is dependent on a number of factors such as aggressiveness, strength, offensive secretions, rate of recruitment of congeners, colony size, etc. The behaviour of an ant should therefore differ according to the type of opponent it encounters. It was demonstrated in Chapter 4 that individuals of *M. scabrinodis* do, in fact, show measurable differences in behaviour towards 5 different species of opponent that commonly occur in the same habitat, and further, that an ant is far more aggressive towards

species of its own genus than towards 3 species of the genus *Lasius*. It has been discussed how competition should be greater between taxonomically similar species, which generally have more similar requirements, than between more remote species. Convergence in behaviour will of course occur between unrelated species occupying similar niches. The habits and requirements of *M. scabrinodis* are more similar to *M. rubra* than to the *Lasius* species. This is an example where interspecific competition is correlated with aggression. Intraspecific fighting in *M. scabrinodis* was less fierce than intrageneric fighting with *M. rubra*. In this example the degree of competition and aggression are not correlated. Thus no sweeping generalisation of the taxonomic relationship and the level of aggression can be made and each type of interaction must be taken on its own merits.

The competition among ants for food and nest site is fierce and much of the interference between colonies takes the form of open aggression. *M. scabrinodis* and *L. flavus* frequently inhabit the same nest mound yet their association has been shown to be far from friendly. The *Myrmica* do not remain in the nest of the hostile *Lasius*, as one might first imagine, by superior aggression. Indeed, their colonies are relatively much smaller, their speed and rate of recruitment is slower and they are intruding in a place of great importance to the *Lasius*. Such factors, as described above, should favour *L. flavus* in colony interactions and quickly lead to the expulsion of the *Myrmica*. The *Lasius* were in fact seen to be far more aggressive than the *Myrmica* in pair encounters. Nevertheless, *M. scabrinodis* can remain in the *L. flavus* nest against hostile opposition from the territory owners. The experiments have shown the highly complex behaviour evolved by *M. scabrinodis* that reduces confrontation and enables their coexistence with *L. flavus*. *M. scabrinodis* is believed to invade the *Lasius* nest for its favourable conditions, to feed on the aphids within the *Lasius* territory and to

prey on the *Lasius* workers and possibly brood. The nests of both *M. rubra* (Elmes, 1974) and *L. niger* (Pontin, 1961) are usually not associated with *L. flavus* and the species have territories which are strongly defended. There are occasions, however, when the species can be found beneath the same stone as *L. flavus* and separated by only a thin wall of soil. Removal of the stone causes fighting. This is another example where the usual territories and intercolonial distances are drastically reduced and where the species have adapted their behaviour to suit a particular ecological situation. The nest site is, presumably, required by both species, neither of which is prepared to relinquish it, thus resulting in a coexistence. Threatening behaviour is believed to be very important in such situations for the species to maintain their nest identity without 'all out' war. The function of the threat posture in communicating the intentions of the animal by chemical means has been proposed and discussed in Chapter 3. The importance of such a function seems to have been neglected in ants. Wroughton (quoted in Wilson, 1971, page 351) describes a *Crematogaster* species robbing a *Holcomyrma* worker of grain by threats. Pontin (1961) could find no evidence of intraspecific fighting in *L. flavus*. Odours released by threatening behaviour would seem to be a possible way for the *Lasius* to maintain their underground feeding territories against intraspecific invaders with least damage to the species. Ritualised intraspecific fighting is a common occurrence in many vertebrates. It has also been shown to occur in a honey-pot ant, *Myrmecocystus* (Holldobler, 1976b). Lorenz (1966) believes that mechanisms inhibiting fighting are essential to survival in lower animals and man alike. The lack of severity of intraspecific combats is recorded in *Tetramorium caespitum* (Wilson, 1971, page 451), *M. rubra* (De Vroey, 1978) and in *M. scabrinodis* here. Behavioural mechanisms that reduce intraspecific fighting would seem then to be widespread in ants.

All behavioural characters, like morphological ones, are evolved as adaptation to environmental factors. Behaviour has no fossil record. A comparative analysis of the living taxonomic units of the genus *Myrmica* here has provided a better understanding of the behavioural and possibly phylogenetic relationship of the 6 species. It has been illustrated how the behavioural relationship of the species to one another was, in many ways, similar to the taxonomic relationship. For example, *M. scabrinodis*, *M. sabuleti* and *M. shencki* are similar to one another in both form and behaviour. *M. rubra* is more similar to *M. sulcinodis* than to the above 3 species again by using both measurements. *M. rubra* and *M. ruginodis*, however, are morphologically very similar but behaviourally quite different. These 2 species have very different habitat requirements (Elmes, 1975, page 180) which is presumably responsible for their divergence in behaviour. This illustrates that while both morphological and behavioural characters have evolved to suit particular ecological needs the 2 processes do not necessarily evolve hand-in-hand.

The comparative and quantitative approach employed throughout this study has permitted a detailed examination of the individual behaviour patterns of some British ants. It has also proved to be a good way of examining the variability of behaviour due to the type of individual and to other influencing factors. By studying individual behaviour patterns it is possible to gain a better understanding of group behaviour. Such studies have been instrumental in gaining a better understanding of the ecological relationship between *M. scabrinodis* and *L. flavus*. The importance of pheromones to intra- and interspecific interactions has been discussed earlier. Our knowledge of the identity of ant pheromones is increasing rapidly. It would, in the light of these recent identifications, be interesting to investigate their effect on actual behavioural responses. For example, in the case of *M. scabrinodis*

and *L. flavus* how particular pheromones may influence individual responses such as THREAT, CONFLICT or ABDOMEN-CURLING and group activity such as 'blocking' behaviour and offensive and defensive strategies. The investigations of this study have been concerned with behaviour within the individual. A sequential analysis of the behavioural responses of *M. scabrinodis* towards both *L. flavus* and *M. rubra* has been made (Moxon, unpublished). However, no detailed studies in ants to date have examined inter-individual behaviour - that is, a step-by-step analysis of how a response shown by one animal influences the following response of its opponent. Such a study would be complex but worthwhile. However institutionalised the societies of both ants and men become, it should not be forgotten that they are composed of and influenced by individuals within them.



APPENDIX.

Tables 1 - 15. Temporal patterning of the responses shown by groups of test animals in experimental encounters. The 30 minute encounters are analysed in 6 x 5 minute periods by the Friedman two-way analysis of variance ( $\chi^2$ ). The associated probability level (P) is given where appropriate (see page 50 for Key).

TABLE 1.

*M. sulcinodis* vs *L. flavus*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi^2$	P	$\chi^2$	P
APPROACH	0.97	N.S.	n.a.	-
AVOID	1.53	N.S.	n.a.	-
MEET	11.43	*	1.93	N.S.
THREAT	8.79	N.S.	8.00	N.S.
CONFLICT	2.63	N.S.	0.63	N.S.
LUNGE	1.87	N.S.	n.a.	-
BITE	2.26	N.S.	n.a.	-
SEIZE	0.54	N.S.	1.74	N.S.
DRAG	0.53	N.S.	0.57	N.S.
STING	3.09	N.S.	4.09	N.S.
CHASE	4.51	N.S.	n.a.	-
FLEE	2.61	N.S.	n.a.	-
GROOM	1.86	N.S.	1.56	N.S.
LOCOMOTION	6.99	N.S.	18.51	**
STILL	7.30	N.S.	9.76	N.S.
ABDOMEN CURLING	1.59	N.S.	2.07	N.S.
AFC. IN LOCOM	5.07	N.S.	5.36	N.S.

TABLE 2.

*M. scabrinodis* vs *L. flavus*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi^2$	P	$\chi^2$	P
APPROACH	2.61	N.S.	n.a.	-
AVOID	4.19	N.S.	n.a.	-
MEET	4.51	N.S.	0.71	N.S.
THREAT	6.06	N.S.	0.90	N.S.
CONFLICT	6.49	N.S.	9.61	N.S.
LUNGE	0.00	N.S.	n.a.	-
BITE	0.00	N.S.	n.a.	-
SEIZE	0.00	N.S.	0.00	N.S.
DRAG	0.00	N.S.	0.00	N.S.
STING	0.00	N.S.	0.00	N.S.
CHASE	0.00	N.S.	n.a.	-
FLEE	0.00	N.S.	n.a.	-
GROOM	7.21	N.S.	1.28	N.S.
LOCOMOTION	5.53	N.S.	5.40	N.S.
STILL	1.60	N.S.	7.56	N.S.
ABDOMEN CURLING	4.06	N.S.	8.67	N.S.

TABLE 3.

*M. scabrinodis* (young) vs *L. flavus*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi^2$	P	$\chi^2$	P
APPROACH	2.11	N.S.	n.a.	-
AVOID	1.24	N.S.	n.a.	-
MEET	4.53	N.S.	4.61	N.S.
THREAT	0.43	N.S.	0.49	N.S.
CONFLICT	0.14	N.S.	0.27	N.S.
LUNGE	0.00	N.S.	n.a.	-
BITE	0.00	N.S.	n.a.	-
SEIZE	0.00	N.S.	0.00	N.S.
DRAG	0.00	N.S.	0.00	N.S.
STING	0.00	N.S.	0.00	N.S.
CHASE	0.00	N.S.	n.a.	-
FLEE	0.00	N.S.	n.a.	-
GROOM	3.26	N.S.	2.43	N.S.
LOCOMOTION	2.97	N.S.	6.40	N.S.
STILL	5.47	N.S.	7.49	N.S.
ABDOMEN CURLING	4.57	N.S.	6.03	N.S.

TABLE 4.

*M. scabrinodis* vs *L. flavus* (young)

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi^2$	P	$\chi^2$	P
APPROACH	3.61	N.S.	n.a.	-
AVOID	1.77	N.S.	n.a.	-
MEET	3.93	N.S.	1.86	N.S.
THREAT	0.86	N.S.	0.96	N.S.
CONFLICT	0.57	N.S.	1.79	N.S.
LUNGE	0.00	N.S.	n.a.	-
BITE	0.00	N.S.	n.a.	-
SEIZE	0.00	N.S.	0.00	N.S.
DRAG	0.00	N.S.	0.00	N.S.
STING	0.00	N.S.	0.00	N.S.
CHASE	0.00	N.S.	n.a.	-
FLEE	0.00	N.S.	n.a.	-
GROOM	1.51	N.S.	1.73	N.S.
LOCOMOTION	6.70	N.S.	7.93	N.S.
STILL	2.37	N.S.	2.01	N.S.
ABDOMEN CURLING	5.19	N.S.	2.34	N.S.

TABLE 5.

*M. scabrinodis* (Hungry) vs *L. flavus*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	6.14	N.S.	n.a.	-
AVOID	0.34	N.S.	n.a.	-
MEET	2.64	N.S.	0.21	N.S.
THREAT	0.44	N.S.	0.86	N.S.
CONFLICT	0.35	N.S.	0.35	N.S.
LUNGE	0.00	N.S.	n.a.	-
BITE	0.00	N.S.	n.a.	-
SEIZE	0.00	N.S.	0.00	N.S.
DRAG	0.00	N.S.	0.00	N.S.
STING	0.00	N.S.	0.00	N.S.
CHASE	0.00	N.S.	n.a.	-
FLEE	0.00	N.S.	n.a.	-
GROOM	5.31	N.S.	2.16	N.S.
LOCOMOTION	5.21	N.S.	10.51	N.S.
STILL	2.73	N.S.	4.51	N.S.
ABDOMEN CURLING	6.70	N.S.	1.19	N.S.

TABLE 6.

*M. scabrinodis* vs *L. flavus*-(9:1 Ratio)

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	46.21	***	n.a.	-
AVOID	0.00	N.S.	n.a.	-
MEET	18.03	**	24.99	***
THREAT	n.a.	-	n.a.	-
CONFLICT	n.a.	-	n.a.	-
LUNGE	0.00	N.S.	n.a.	-
BITE	0.35	N.S.	n.a.	-
SEIZE	0.35	N.S.	0.40	N.S.
DRAG	0.00	N.S.	0.00	N.S.
STING	0.00	N.S.	0.00	N.S.
CHASE	0.60	N.S.	n.a.	-
FLEE	0.00	N.S.	n.a.	-
GROOM	0.81	N.S.	5.91	N.S.
LOCOMOTION	4.80	N.S.	16.00	**
STILL	6.38	N.S.	32.96	***
ABDOMEN CURLING	11.21	*	4.00	N.S.

TABLE 7.

*M. scabrinodis* vs *L. flavus* (Dead)

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	0.05	N.S.	n.a.	-
AVOID	6.35	N.S.	n.a.	-
MEET	3.75	N.S.	0.45	N.S.
THREAT	0.05	N.S.	0.20	N.S.
CONFLICT	0.20	N.S.	0.60	N.S.
LUNGE	1.05	N.S.	n.a.	-
BITE	0.70	N.S.	n.a.	-
SEIZE	1.40	N.S.	0.60	N.S.
DRAG	0.50	N.S.	0.60	N.S.
STING	0.15	N.S.	0.05	N.S.
CHASE	n.a.	N.S.	n.a.	-
FLEE	0.00	N.S.	n.a.	-
GROOM	1.55	N.S.	0.06	N.S.
LOCOMOTION	10.05	N.S.	2.15	N.S.
STILL	0.65	N.S.	2.85	N.S.
ABDOMEN CURLING	0.15	N.S.	0.05	N.S.

TABLE 8.

*M. scabrinodis* vs *L. niger* (Dead)

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	0.45	N.S.	n.a.	-
AVOID	2.15	N.S.	n.a.	-
MEET	4.20	N.S.	2.15	N.S.
THREAT	2.15	N.S.	2.45	N.S.
CONFLICT	0.00	N.S.	0.00	N.S.
LUNGE	0.00	N.S.	n.a.	-
BITE	0.15	N.S.	n.a.	-
SEIZE	0.20	N.S.	0.65	N.S.
DRAG	0.65	N.S.	1.40	N.S.
STING	0.20	N.S.	0.20	N.S.
CHASE	n.a.	-	n.a.	-
FLEE	0.00	N.S.	n.a.	-
GROOM	1.05	N.S.	3.75	N.S.
LOCOMOTION	4.65	N.S.	0.45	N.S.
STILL	0.05	N.S.	0.15	N.S.
ABDOMEN CURLING	0.00	N.S.	0.00	N.S.

TABLE 9.

*M. scabrinodis* vs *L. umbratus*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	2.73	N.S.	n.a.	-
AVOID	0.34	N.S.	n.a.	-
MEET	12.40	*	1.69	N.S.
THREAT	3.30	N.S.	3.57	N.S.
CONFLICT	6.31	N.S.	4.71	N.S.
LUNGE	1.00	N.S.	n.a.	-
BITE	0.39	N.S.	n.a.	-
SEIZE	1.37	N.S.	1.37	N.S.
DRAG	0.34	N.S.	0.34	N.S.
STING	0.39	N.S.	0.40	N.S.
CHASE	0.86	N.S.	n.a.	-
FLEE	5.27	N.S.	n.a.	-
GROOM	0.29	N.S.	0.90	N.S.
LOCOMOTION	3.20	N.S.	7.19	N.S.
STILL	0.39	N.S.	7.97	N.S.
ABDOMEN CURLING	4.89	N.S.	0.11	N.S.

TABLE 10.

*M. scabrinodis* vs *L. niger*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	11.33	*	n.a.	-
AVOID	0.66	N.S.	n.a.	-
MEET	10.86	N.S.	6.97	N.S.
THREAT	14.47	*	5.83	N.S.
CONFLICT	10.04	N.S.	8.90	N.S.
LUNGE	2.20	N.S.	n.a.	-
BITE	0.86	N.S.	n.a.	-
SEIZE	1.46	N.S.	0.77	N.S.
DRAG	0.74	N.S.	0.74	N.S.
STING	0.86	N.S.	0.36	N.S.
CHASE	4.91	N.S.	n.a.	-
FLEE	0.21	N.S.	n.a.	-
GROOM	1.26	N.S.	1.83	N.S.
LOCOMOTION	8.93	N.S.	5.56	N.S.
STILL	4.60	N.S.	1.27	N.S.
ABDOMEN CURLING	3.03	N.S.	4.53	N.S.

TABLE 11.

*M. scabrinodis* vs *M. rubra*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	11.30	*	n.a.	-
AVOID	2.01	N.S.	n.a.	-
MEET	17.53	**	10.53	N.S.
THREAT	10.60	N.S.	10.04	N.S.
CONFLICT	0.90	N.S.	0.64	N.S.
LUNGE	4.79	N.S.	n.a.	-
BITE	2.79	N.S.	n.a.	-
SEIZE	11.17	*	10.04	N.S.
DRAG	14.04	*	4.77	N.S.
STING	2.99	N.S.	2.86	N.S.
CHASE	17.97	**	n.a.	-
FLEE	0.40	N.S.	n.a.	-
GROOM	6.65	N.S.	6.77	N.S.
LOCOMOTION	14.04	*	13.54	*
STILL	0.43	N.S.	0.50	N.S.
ABDOMEN CURLING	0.43	N.S.	0.44	N.S.

TABLE 12.

*M. scabrinodis* vs *M. scabrinodis*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	7.71	N.S.	n.a.	-
AVOID	0.00	N.S.	n.a.	-
MEET	0.47	N.S.	9.76	N.S.
THREAT	7.41	N.S.	6.24	N.S.
CONFLICT	0.86	N.S.	0.86	N.S.
LUNGE	0.77	N.S.	n.a.	-
BITE	0.71	N.S.	n.a.	-
SEIZE	6.32	N.S.	17.29	**
DRAG	3.14	N.S.	3.04	N.S.
STING	2.69	N.S.	3.47	N.S.
CHASE	0.00	N.S.	n.a.	-
FLEE	0.00	N.S.	n.a.	-
GROOM	0.34	N.S.	1.36	N.S.
LOCOMOTION	0.99	N.S.	1.00	N.S.
STILL	1.40	N.S.	5.09	N.S.
ABDOMEN CURLING	0.34	N.S.	0.34	N.S.

TABLE 13.

*M. sabuleti* vs *L. flavus*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	0.86	N.S.	n.a.	-
AVOID	2.27	N.S.	n.a.	-
MEET	1.06	N.S.	13.37	*
THREAT	0.35	N.S.	0.35	N.S.
CONFLICT	0.44	N.S.	0.54	N.S.
LUNGE	0.00	N.S.	n.a.	-
BITE	0.00	N.S.	n.a.	-
SEIZE	0.00	N.S.	0.00	N.S.
DRAG	0.00	N.S.	0.00	N.S.
STING	0.00	N.S.	0.00	N.S.
CHASE	0.00	N.S.	n.a.	-
FLEE	0.00	N.S.	n.a.	-
GROOM	2.06	N.S.	1.54	N.S.
LOCOMOTION	5.89	N.S.	7.66	N.S.
STILL	2.77	N.S.	2.06	N.S.
ABDOMEN CURLING	1.59	N.S.	2.43	N.S.

TABLE 14.

*M. shencki* vs *L. flavus*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	0.81	N.S.	n.a.	-
AVOID	0.34	N.S.	n.a.	-
MEET	5.99	N.S.	0.50	N.S.
THREAT	0.00	N.S.	0.0	N.S.
CONFLICT	1.26	N.S.	1.00	N.S.
LUNGE	0.00	N.S.	n.a.	-
BITE	0.00	N.S.	n.a.	-
SEIZE	0.00	N.S.	0.00	N.S.
DRAG	0.00	N.S.	0.00	N.S.
STING	0.00	N.S.	0.00	N.S.
CHASE	0.00	N.S.	n.a.	-
FLEE	3.30	N.S.	n.a.	-
GROOM	0.34	N.S.	0.34	N.S.
LOCOMOTION	5.34	N.S.	7.29	N.S.
STILL	6.90	N.S.	8.87	N.S.
ABDOMEN CURLING	0.34	N.S.	0.34	N.S.

TABLE 15.

*M. rubra* vs *L. flavus*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	0.73	N.S.	n.a.	-
AVOID	9.24	N.S.	n.a.	-
MEET	32.98	***	8.00	N.S.
THREAT	21.77	***	15.19	**
CONFLICT	7.34	N.S.	7.09	N.S.
LUNGE	1.37	N.S.	n.a.	-
BITE	0.00	N.S.	n.a.	-
SEIZE	4.97	N.S.	3.19	N.S.
DRAG	2.97	N.S.	2.61	N.S.
STING	2.89	N.S.	1.80	N.S.
CHASE	0.00	N.S.	n.a.	-
FLEE	5.50	N.S.	n.a.	-
GROOM	0.90	N.S.	0.90	N.S.
LOCOMOTION	12.67	*	8.74	N.S.
STILL	11.76	*	1.59	N.S.
ABDOMEN CURLING	4.57	N.S.	10.20	N.S.

TABLE 16.

*M. ruginodis* vs *L. flavus*

BEHAVIOURAL RESPONSE	OCCURRENCE		DURATION	
	$\chi r^2$	P	$\chi r^2$	P
APPROACH	2.07	N.S.	n.a.	-
AVOID	4.87	N.S.	n.a.	-
MEET	8.96	N.S.	0.44	N.S.
THREAT	1.77	N.S.	1.77	N.S.
CONFLICT	0.34	N.S.	0.36	N.S.
LUNGE	0.36	N.S.	n.a.	-
BITE	0.40	N.S.	n.a.	-
SEIZE	0.43	N.S.	0.44	N.S.
DRAG	0.43	N.S.	0.44	N.S.
STING	0.43	N.S.	0.43	N.S.
CHASE	0.34	N.S.	n.a.	-
FLEE	0.88	N.S.	n.a.	-
GROOM	6.40	N.S.	5.73	N.S.
LOCOMOTION	6.49	N.S.	1.79	N.S.
STILL	2.91	N.S.	0.97	N.S.
ABDOMEN CURLING	2.93	N.S.	2.24	N.S.

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