S.-Afr. Tydskr. Dierk. 1991, 26(4)

# Quantifying tasks and roles in insect societies

M.H. Villet
Department of Zoology, University of the Witwatersrand, P.O. Wits, 2050 Republic of South Africa

*Received 18 February 1991; accepted 15 May 1991*

When setting out a framework for the exploration of a subject, it is necessary to define terms to represent specific concepts, and to refine them as knowledge of the subject grows. It is a great advantage if stipulative definitions are also operational definitions, since this makes methods of quantification obvious. The concepts of *tasks* and *roles* are central to studies of organization of labour in insect societies, but their application has sometimes been problematic. Here their definitions are reviewed, and appropriate methods of quantification and analysis are outlined. These involve correspondence analysis and Markov chain analysis of transition probability matrices to study the organization of behaviour into tasks, and correspondence analysis of ethograms made by scan sampling to investigate the roles filled by the workers.

Wanneer 'n raamwerk saamgestel word vir die bestudering van 'n onderwerp, is dit nodig om die terme wat spesifieke konsepte verteenwoordig to definieer en te verfyn namate meer inligting oor die onderwerp ingewin word. Dit is baie voordelig as bepalende definisies ook bedryfdefinisies kan wees, aangesien dit die metode van kwantifisering duidelik maak. Die konsepte van *pligte* en *verantwoordelikhede* is sentraal aan studies oor die organisasie van werk in insekkolonies, maar hul toepassing is soms problematies. Hul definisies word hier bespreek en paslike metodes van kwantifiserring word uitgestip. Dié metodes behels ooreenstemmings-analise en Markov kettinganalise van transisie waarskynlikheidsmatrikse om die organisering van gedrag in pligte te bestudeer en ooreenstemmingsanalise van etogramme, verkry deur oorsigtelike steekproefneming om die rolle wat deur die werkers vervul word, te ondersoek.

## Introduction

Studies of division of labour in insect societies are concerned with the way that these societies meet the contingencies, or tasks, that they face. The notion of *role* is important in these studies because roles describe the social function of individuals in their colony (Jeanne 1986; Villet 1991a). Responsibility for the execution of tasks is, conceptually, implicitly divided into roles that are filled by colony members (Oster & Wilson 1978). The set of roles found in a colony constitute that colony's behavioural profile, which is seen as being adapted to the contingencies facing it (Wilson 1984; Walker & Stamps 1986).

Jeanne (1986) explored the distinction between the organization of labour itself and the organization of the workers performing it. He showed that it is logically possible to have partitioning of tasks without division of labour, but not *vice versa*. The partitioning of tasks allows for selection for greater efficiency of execution, through changes in the time spent on each task. This was termed *ergonomic selection*, and was associated with the evolution of increasing behavioural specialization, terminating in physical polyethism, where differences in physical form reflect differences in social function. Ergonomic selection affects the relationship between form and function.

The sequence in which tasks are performed by workers, i.e. the organization of the workers, allows for selection for an increase in worker longevity, based on the risk attached to each task. Such *demographic selection* was associated with the evolution of age polyethism (Jeanne 1986), where workers pass through a series of social roles as they mature, ending in the most risky. The time frame of roles is of the order of days or weeks, while that of tasks is minutes or hours (Jaisson, Fresneau & Lachaud 1988; Jeanne 1986).

Because they are logically distinct, both tasks and roles need to be quantified to gain a thorough characterization of labour in an insect society. Calabi & Rosengaus (1988) have raised questions about the usefulness of the concept of roles in studies of social insects. Their problems seem to arise from weaknesses in the commonly-used operational definitions of this concept, a problem that besets many aspects of the quantification of social behaviour (Jaisson *et al.* 1988), rather than from any flaw in the concept. From a brief examination of the definitions of 'task' and 'role', this work pursues two themes to develop a rigorous methodology for their quantification: proposing guidelines for appropriate sampling methods and sample sizes; and a critical review of appropriate analytical techniques. These approaches are meant only to describe a colony's roles and tasks, serving as the basis for more sophisticated studies into social mechanisms (e.g. Seeley 1982; Jeanne, Downing & Post 1988).

In the following discussion, it is assumed that the activity of an animal can be decomposed into a set, or *repertoire*, of relatively stereotyped units, termed behaviours. The exact degree of stereotypy, and hence the subjective definition of each particular behaviour, depends on the purpose of the study (Slater 1976; Jaisson *et al.* 1988). Each occurrence of a behaviour is termed an act (Fagen & Goldman 1977; Slater 1976).

## Definitions

*Tasks* describe the organization of behaviour into functional groups (Jeanne 1986). They are stipulatively defined as groups of behaviours that serve a common goal (Hölldobler & Wilson 1990: 301; Jeanne 1986; Jeanne *et al.* 1988; Seeley 1982), or that achieve some purpose, or meet some contingency, for the colony (Oster & Wilson 1978: 326). For example, several behaviours directed towards brood might be tightly linked into a single task, that of brood care (Herbers & Cunningham 1983). Some tasks may comprise only one behavioural category, such as behaviours related to nest building and cleaning, which often constitute independent tasks in themselves (Jeanne 1986; Wilson 1980: 144). Tasks are categorical, discontinuous and mutually exclusive, a property reflected in some definitions of the term (Oster & Wilson 1978). The operational definition of specific tasks is integral to studies of the organization of labour in a given species of social insect.

*Roles*, on the other hand, describe the functional organization of colony members to carry out tasks (Jeanne 1986; Villet 1991a). In species that show division of labour, certain tasks are performed by one group of colony members, more or less excluding other members, which then perform other tasks. The result is a partitioning of labour in the colony (Hölldobler & Wilson 1990: 642; Jeanne *et al.* 1988; Seeley 1982). Thus, the behaviour of each individual fulfils a relatively specific, specialized social function, or role, which is characterized by frequent performance of some behaviours and rare performance of others. Some tasks may fall to a single individual. For example, reproduction is often monopolized by a single queen in each colony. Where several individuals show similar behaviour biases, they form a group that is characterized by that shared 'task set' (Seeley 1982) or role (Jeanne *et al.* 1988).

*Role* has been considered synonymous with caste (Buschinger 1987), or at least regarded as implicitly equivalent (Oster & Wilson 1978; Hölldobler & Wilson 1990). However, it is useful to use these terms to denote the function and form, respectively, of a social insect, and since form and function are not heuristically equivalent, it may be better to make a distinction between *role* and *caste* (Villet 1991a).

Workers may include one or more tasks in their roles (in varying ratios), and often move from one role to another during their lifetimes. This difference in time frames is important in defining the time spans over which samples should be collected for quantifying tasks and roles.

## Quantifying tasks

The definition of tasks as groups of linked behaviours implies that the behaviours are not statistically independent of one another, and this can serve as the basis for their operational definition.

Analysis of the directed, single-step transitions between behaviours was suggested as a means of characterizing tasks (Jeanne 1986). This approach assumes that behaviours that are linked in function will have high probabilities of following one another, especially compared to functionally unrelated behaviours. They should form groups characterized by high transition probabilities, and linked to other such groups by low probabilities. Such links may be formed through behaviours that are not (parts of) tasks, such as walking from one task to another. An important assumption in using such a matrix is that of stationariness: the probability of a particular behaviour or transition should not be affected by the passage of time. This assumption is probably unrealistic because of changing environmental conditions and age polyethism (Calabi & Traniello 1989a, 1989b; Gordon 1989), but provided that such limitations are recognized, this method can be useful.

Focal animal sampling (Altmann 1974) has been used to collect data for transition analysis (Herbers & Cunningham 1983; Calabi & Rosengaus 1988; Villet 1991b). This technique involves recording a long sequence of acts (about 30 min) from each of as many members of a colony as is practically possible. When any act is followed by any other, a directed transition between them is scored. Obviously, no behaviour can follow itself, and the transition scores of any pair of behaviours will probably differ according to which behaviour is first. Since the emphasis is on obtaining a sample of transitions for every behaviour in a repertoire, rather than a sample of every worker's behaviour, transition analysis allows sub-sampling of a colony, which is useful when dealing with large colonies. A risk taken in sampling different individuals is that their behaviour may not be homogenous. In fact, this is to be expected, since different individuals will probably perform a spectrum of roles in their colony. However, this does not affect studies that aim merely to describe tasks, rather than to explore underlying patterns of organization.

In a repertoire of $R$ different behavioural categories, the sample size needed to obtain an average of one sample of each transition would be $R \times R = R^2$ transitions. To generate enough replicates of each transition, this sample would have to be repeated at least six times (Fagen & Young 1978), i.e. a sample of $6\,R^2$ transitions or more. In focal animal samples, very rare behaviours (acts for which fewer than six transitions were recorded) are better left out of the matrix because they show very high associations with their neighbouring behaviours that are an artifact of their rarity in the sample. Since the repertoires of social insects contain 20–70 behaviours (Cole 1985; Villet 1990), sample sizes of 3 200–12 800 acts provide good coverage for most transition analyses. Logical zeros (impossible transitions) can be subtracted from the sample, so that, given $Z$ impossible transitions, samples should contain some $8(R^2 - Z)$ acts. The effect of clustering (i.e. into tasks) on these sampling guidelines is unclear (Fagen & Young 1978), but it might cause only under-representation of rare linkages in focal animal samples.

Transition scores are entered into an asymmetrical, $R \times R$, transition frequency matrix (Oster & Wilson 1978), in which the behaviours in the columns are in the same (arbitrary) order as those in the rows. The matrix is then converted to a transition probability matrix. The probability, $P_{i \to j}$, of a directed transition between behaviours $i$ and $j$ is

$$P_{i \to j} = n_{i \to j} / n_t \qquad 1$$

where $n_{i \to j}$ is the number of times the particular transition from behaviour $i$ to behaviour $j$ was recorded and $n_t$ is the total number of transitions in the matrix. The row and column totals of a transition probability matrix should all be 1,0 because they are probabilities. Using focal animal sampling, this can be difficult to achieve because one has to sample from different individuals in order to sample all behaviours, and this causes breaks in the sequence, and unequal sampling of initial and terminal behaviours. However, iterative proportional fitting procedures (Chilko 1983; van der Heijden 1986) are available for standardizing such matrices.

The least rigorous analysis of such a matrix involves rearranging its rows and columns until blocks or clusters of behaviours with high transition probabilities appear (Herbers & Cunningham 1983). The only restriction is that the order of the behaviours in the columns must be the same as in the rows when the shuffle is completed. The matrix is then examined for groups of high behavioural transition probabilities, since behaviours that are closely associated are not statistically independent, and should show higher transition probabilities than behaviours that are associated randomly. The rows and columns bounding the blocks define the groups of interest. Using this technique, high and low transition probabilities must be designated relative to subjectively derived expected values.

Objective expected probabilities, $E_{i \to j}$, for randomly associated, directed transitions can be calculated by contingency table methods from

$$E_{i \to j} = (n_{i \to} / n_t)(n_{\to j} / (n_t)) \qquad 2$$

where $n_i$ is the number of acts of the leading behaviour, $n_j$ is the number of acts of the following behaviour, and $n_t$ is the total number of transactions sampled. To find statistical significance strong or weak associations, differences between observed and expected values can be assessed using a $\chi^2$ test (Sokal & Rohlf 1981; van der Heijden, de Vries & van Hooff 1990).

The presence of impossible transitions (termed logical zeros) in a transition matrix can complicate the calculation of expected values by traditional contingency table methods (Altmann & Altmann 1977; Colgan & Smith 1978; Fagen & Young 1978). These transitions can be circumvented by conducting the contingency analysis on blocks of behaviours, rather than on cells of the matrix, but the approach remains subjective in the way that blocks are defined. Instead, iterative fitting procedures can be used to provide independent values for these cells, thus preventing them from affecting the patterns of association in the remaining cells (van der Heijden 1986).

Multivariate analysis of a transition matrix can be conducted using correspondence analysis (van der Heijden *et al.* 1990). This method involves using $\chi^2$ measures of difference to calculate associations between rows and between columns of the matrix. These sets of measures can be projected into the same $(R - 1)$-dimensional Euclidean space, providing a pictorial representation of the association between the row and column variables, which are, in this case, the leading and following behaviours. By using modified transition matrices, this pattern can be interpreted further with correspondence analysis (van der Heijden *et al.* 1990).

Hierarchical cluster analysis provides another multivariate approach to interpreting of the transition probability matrix (Hubert 1973), yielding an exact measure of the linkage between (groups of) behaviours. The results can be expressed graphically as a dendrogram. Unfortunately, cluster analysis does not offer an indication of the statistical significance of groups: the levels of association defining independent tasks must be decided by the asymmetrical contingency table analysis outlined above. Some groups may be found to contain behaviours that would not be considered 'labour' (e.g. Villet 1990, 1991b), which might indicate that the other behaviours in the cluster are not linked by their function into a single task. For these reasons, this method has far less appeal than correspondence analysis as an analytical tool for defining tasks.

The foregoing statistical methods are primarily descriptive. To gain deeper understanding of the processes structuring a transition matrix, it has been suggested (Oster & Wilson 1978) that it be treated as a Markov chain (Cane 1978; Castellan 1979). The models most useful to ethology are non-stationary, ascending-order Markov chains (Oden 1977). Non-stationary models do not assume that the occurrence of one transition has no effect on the probability of any other (stability), or that the probabilities of each behaviour and their transition probabilities are constant (stationary) over time (Oden 1977). This is advantageous because these assumptions seldom hold true over periods longer than a few days. For instance, as brood matures, the changing proportions of each stage will affect the frequency of brood-related behaviours. However, transition matrices are implicitly stationary, restricting the validity of the results of Markov chain analysis to the period of sampling.

In a first-order Markov chain, the probability of a behaviour following another depends only on the identity of the previous act. Similarly, in an $n^{\text{th}}$ order chain, this probability depends on $n$ previous acts, and is independent of any before them. In reality, however, some behaviours may appear cyclically, with a high Markov order (such as feeding or excretion), while others have low-order dependence on events that occur more randomly (like defending the nest). Ascending-order Markov chain analysis overcomes these problems and offers some insight into the interdependence of behaviours which are separated by intervening acts.

The sampling argument outlined for single-step transition analysis can be extended to yield the general guideline of a sample size of $8(R^{n+1} - Z)$ acts to construct an $n^{\text{th}}$-order Markov chain (Fagen & Young 1978).

Because the acts in the sample must be consecutive, transition sampling can be combined with time budget sampling. The transition matrix can then be used to assess energy flow in the colony if the holding times on the major diagonal of the matrix are filled in from the time budget (Oster & Wilson 1978: 123). If time is measured in seconds the resulting matrix contains second-to-second transition frequencies, and can be analysed using continuous time Markov chain methods (Haccou 1986; Metz, Dienske, de Jonge & Putters 1983).

The use of video tape recording greatly facilitates this type of sampling, allowing one to time behaviours more accurately and to collect data from different animals simultaneously. Such ergonomic studies require very large samples: to fill out the statistical distribution of durations of each behaviour adequately, about 30 observations per behaviour are needed (Fagen & Young 1978), implying a minimum sample of $30(R^2 - Z)$ acts.

Finally, information theory has been applied to behavioural data to test for non-independence between categories of behaviour (e.g. Losey 1978). This approach primarily detects global interactions, but can reveal individual dependencies (van der Bercken & Cools 1980). It generally needs data about the durations of behaviours in order to draw valid conclusions (Haccou 1986; Metz *et al.* 1983).

Appropriate data sets would be of the same sizes, and obtained by the same methods, as time budget samples.

## Quantifying roles

It has been suggested that transition analysis could be used to characterize roles (Oster & Wilson 1978: 122). Since transition analysis takes into account only the sequences of behaviours, and not the identity of the workers performing them, it cannot provide information on the social function of individuals. Although this was not their reason, Calabi & Rosengaus (1988) were correct when they concluded that 'one cannot use transition probabilities alone to define roles'.

If roles are characterized by biases in the frequencies with which different behaviours are performed, these biases can be shown by comparing the ethograms (Oster & Wilson 1978) of individual colony members. The definition of behaviours depends on the level of stereotypy required by a study (Slater 1976). The subjectivity of such definitions has been a major criticism of the use of ethograms (e.g. Jaisson *et al.* 1988; but *cf.* Hölldobler & Wilson 1990). Transition analysis might help to homogenize levels of stereotypy within a study by linking behaviours that are not (parts of) tasks into groups that can be replaced by a single behavioural category. This remains to be tested.

The acts recorded to construct an ethogram should be sampled randomly and independently (Jaisson *et al.* 1988). If the ethograms of each individual or group are to be compared rigorously, the number of ants sampled from each one, and sampling durations, should be equal. These criteria are best met by scan sampling (Altmann 1974) over a few days. Scan sampling entails marking colony members (Corbara, Lachaud, Fresneau & Provent 1988; Jaisson *et al.* 1988) so that they can be individually recognized, and recording one act from each in turn, until the required sample size is reached. The total duration of sampling should be shorter than the duration of the shortest phase in the pattern of age polyethism, otherwise more than one role may be sampled from the same animal. There is some evidence that these changes may be gradual and continuous in ants (Calabi & Traniello 1989a, 1989b; Gordon 1989), but a more discrete pattern of roles was found in a species of wasp (Jeanne *et al.* 1988).

The thoroughness of an ethogram in representing the behaviour of an individual or a colony is termed its sample completeness. This measure can be calculated using the Fagen-Goldman method (Fagen & Goldman 1977). However, this statistic assumes as its null model that there are no constraints imposed on the behaviour of individuals, for instance by their environment. Since the behaviour of social insects is markedly influenced by both the structure of the colony and its environmental conditions (e.g. Calabi & Traniello 1989a, 1989b; Gordon 1989), the results of this calculation are valid only within the limitations of the social and environmental context in which the data were collected. This method offers a *post hoc* assessment of whether a sample size is adequate, but has never been tested on individuals.

The effect of different sample sizes on correspondence analysis of scan samples has been studied, but no optimal or smallest sample size was suggested (Corbara *et al.* 1988). Empirically, samples of 25 acts per ant were too small; 50 or 66 acts per ant gave results comparable to samples of 400 acts per ant (Corbara *et al.* 1988). Part of this convergence might have been due to a concomitant increase in sampling frequency, which was an uncontrolled effect in this study. If samples are taken too frequently, single acts of long duration may be sampled twice. Sampling every half hour or longer should generally prevent this. A comparable lower limit to sample size can be derived theoretically. In ants, about 20–55% of acts are related to tasks (Calabi & Rosengaus 1988; Villet 1990, 1991b). Assuming an average of 40%, a sample of 50 or more acts from one individual should, on average, yield 20 acts that belong to a task. In a sample of 20 tasks, if one is not characteristic of an individual's role, it will cause only a 5% error. If the percentage of task-related acts is known, the appropriate sample size can be calculated.

It is important to include non-tasks in the sample, because they characterize the repertoire of some individual ants (Corbara *et al.* 1988; Calabi & Rosengaus 1988; Jaisson *et al.* 1988; Villet 1991b). Ideally, every member of a colony should be sampled. This ideal can be met relatively easily for colonies of fewer than 100 members, but is unrealistic for larger colonies. Representative sub-samples of at least 60 randomly-selected workers will probably represent all roles, even in species with complex behavioural repertoires, without subjecting the stamina of the observer to stress.

The similarity of workers' ethograms gathered by scan sampling can be assessed by some form of hierarchical cluster analysis (Jaissan *et al.* 1988). The clustering criterion or algorithm should be chosen carefully, since some will produce more clusters than others (de Ghett 1978), and studies that use different algorithus cannot be compared rigorously. Certain types of results may be artifactual products of the properties of the chosen algorithm rather than of the structure of the data (Cormack 1971). The method is also open to criticism because the boundaries of roles must be defined arbitrarily and the roles characterized *post hoc*: if the initial ethograms are of equal sizes, roles can be defined by designating a suitable, but arbitrarily-chosen degree of similarity as a cut-off level (e.g. Jaisson *et al.* 1988). The resulting pattern of similarities can be clearly expressed as a dendrogram, an easily digested form of presentation, but one that may oversimplify multi-dimensional data since it is one-dimensional.

The social function of groups defined by cluster analysis can also be interpreted by drawing a frequency histogram for each task in each worker's ethogram, keeping the workers in the order defined by the analysis. By superimposing the mean level of performance of the task in the colony (i.e. the mean for all individuals), the behaviour of (groups of) individuals can be examined for biases (Corbara, Lachaud & Fresneau 1989; Jaisson *et al.* 1988).

In order to assess the effects of other variables on roles, details such as age or body size, caste or reproductive status can be added to these diagrams as coded symbols, or, in the case of age or size measurements, plotted on separate, similarly ordered histograms (e.g. Corbara *et al.* 1989; Jaisson *et al.* 1988).

Correspondence analysis (Greenacre 1984; van der Heijden *et al.* 1990) and the various forms of factor anaysis (Frey & Pimentel 1978) are more statistically robust and reproducible multivariate techniques than cluster analyses. They also have the advantage of providing confidence boundaries for groups, and the results can be presented as two- or three-dimensional plots of components or factor scores. However, none of these multivariate methods make reference to any null model, and none has any absolutely reliable aids for interpretating their results. There are several helpful tools for the interpretation of factor analyses (Frey & Pimentel 1978), and correspondence analysis provides a pattern of similarities between the organization of the row and column variables, as well as several measures of association (Greenacre 1984; van der Heijden *et al.* 1990). Factor analysis makes use of matrices of correlation coefficients. There are several types of correlation coefficient, and to the extent that the choice between them is arbitrary, factor analyses are less reproducible than correspondence analyses.

## Conclusion

The definition of tasks is integral to analyses of the structure of the labour needs of a colony, and allows the compaction of a large repertoire of behaviours into a smaller nunber of categories for other studies. The simplest and most useful method involves the construction of a transition probability matrix, and its analysis by correspondence analysis. If more insight into the organizing principles of the matrix is required, non-stationary, ascending-order Markov chain analysis can be applied. Suitable sample sizes are in the range of 6–30 times the square of the number of acts in the repertoire, and much larger for continuous time Markov chain models.

The description of roles is a simple way of quantifying the organization of a work force in terms of the functions that each individual performs. It provides a relatively direct abstraction of the pattern of division of labour in a colony. Correspondence analysis provides an easily interpreted illustration of this pattern. Hierarchical cluster analysis provides a more categorical pattern, but the choice of grouping algorithms and interpretive measures is rather arbitrary. Furthermore, at least in ants, gradual changes in the behaviour of individuals create a continuum of social functions; attempts to define categories in this spectrum are more or less contrived. However, interpeted loosely, the results help to form an abstract picture of the organization of the colony.

## Acknowledgements

Thanks are due to Neil Caithness and my referees for contributing to the development of the manuscript. This work was financed by the Department of Zoology, University of the Witwatersrand, the Council for Scientific and Industrial Research, and the Foundation for Research Development.

## References

ALTMANN, J. 1974. Observational study of behaviour: sampling methods. *Behaviour* 49: 227–267.

ALTMANN, S. & ALTMANN, J. 1977. On the analysis of rates of behaviour. *Anim. Behav.* 25: 364–372.

BUSCHINGER, A. 1987. Polymorphism and reproductive division of labour in advanced ants. In: Chemistry and biology of social insects. (Eds) J. Eder & H. Rembold), pp. 257–258. Verlag J. Peperny, München.

CALABI, P. & ROSENGAUS, R. 1988. Interindividual differences based on behaviour transition probabilities in the ant *Camponotus sericeiventris*. In: Interindividual behavioral variability in social insects. (Ed.) R. Jeanne), pp. 61–89. Westview Press, Boulder, Colorado.

CALABI, P. & TRANIELLO, J. 1989a. Social organisation in the ant *Pheidole dentata:* physical and temporal caste ratios lack ecological correlates. *Behav. Ecol. Sociobiol.* 24: 69–78.

CALABI, P. & TRANIELLO, J. 1989b. Behavioural flexibility in age castes of the ant *Pheidole dentata*. *J. Insect Behav.* 2: 663–677.

CANE, V. 1978. On fitting low-order Markov chains to behavioural sequences. *Anim. Behav.* 26: 332–338.

CASTELLAN, N. 1979. The analysis of behavioural sequences. In: The analysis of social interactions: methods, analysis and illustrations. (Ed.) R. Cairns, pp. 81–116. Lawrence Erlbaum, Hillsdale, New Jersey.

CHILKO, D. 1983. The IPFPHC procedure. In: SUGI supplemental library user's guide 1983 Edition. (Ed.) S. Joyner, pp. 131–144. SAS Institute Incorporated, Cary, North Carolina.

COLE, B. 1985. Size and behavior in ants: constraints on complexity. *Proc. Natl. Acad. Sci. USA*. 82: 8548–8551.

COLGAN, P. & SMITH, J. 1978. Multidimensional contingency table analysis. In: Quantitative Ethology (Ed.) P. Colgan, pp. 145–174. Wiley, New York.

CORBARA, B., LACHAUD, J. & FRESNEAU, D. 1989. Individual variability, social structure and division of labour in the ponerine ant *Ectatomma ruidum* Roger (Hymenoptera, Formicidae). *Ethology* 82: 89–100.

CORBARA, B., LACHAUD, J., FRESNEAU, D. & PROVENT, B. 1988. L'echantillonnage par releve ponctuel pour l'etude de l'organisation sociale des fourmis: limites et optimisation. *Actes Coll. Insectes Soc.* 4: 127–134.

CORMACK, R. 1971. A review of classification. *J. Royal Statist. Soc.* A 134: 321–367.

DE GHETT, V. 1978. Hierarchical cluster analysis. In: Quantitative ethology, (Ed.) P. Colgan, pp. 115–144. Wiley, New York.

FAGEN, R. & GOLDMAN, R. 1977. Behavioural catalogue analysis methods. *Anim. Behav.* 25: 261–274.

FAGEN, R. & YOUNG, D. 1978. Temporal patterns of behaviour: durations, intervals, latencies and sequences. In: Quantitative ethology. (Ed.) P. Colgan, pp. 79–114. Wiley, New York.

FREY, D. & PIMENTEL, R. 1978. Principal component analysis and factor analysis. In: Quantitative methods in the study of animal behaviour. (Ed.) B. Haslet, pp. 219–245. Academic Press, New York.

GORDON, D. 1989. Dynamics of task switching in harvester ants. *Anim. Behav.* 38: 194–204.

GREENACRE, M. 1984. Theory and applications of correspondence analysis. Academic Press, London. 364 pp.

HACCOU, P. 1986. Analysis of behaviour by means of continuous time Markov chain models and thier generalizations. In: Quantitative models in ethology. (Eds) P. Colgan & R. Zayan, pp. 81–96. Privat, Toulouse.

HERBERS, J. & CUNNINGHAM, M. 1983. Social organisation in *Leptothorax longispinosus* Mayr. *Anim. Behav.* 31: 759–771.

HÖLLDOBLER, B. & WILSON, E. 1990. The Ants. Springer Verlag, Berlin.

HUBERT, L. 1973. Min and max hierarchical clustering using asymmetric similarity measures. *Psychometrika* 38: 63–72.

JAISSON, P., FRESNEAU, D. & LACHAUD, J. 1988. Individual traits in social behavior in ants. In: Interindividual behavioral variability in social insects. (Ed.) R. Jeanne, pp. 1–51. Westview Press, Boulder, Colorado.

JEANNE, R. 1986. The evolution of the social organisation of work in social insects. *Monitore zool. ital. (N.S.)* 20: 119–133.

JEANNE, R., DOWNING, H. & POST, D. 1988. Age polyethism and individual variation in *Polybia occidentalis*, an advanced eusocial wasp. In: Interindividual behavioral variability in social insects. (Ed.) R. Jeanne, pp. 323–357. Westview Press, Boulder, Colorado.

LOSEY, G. 1978. Information theory and communication. In: Quantitative ethology (Ed.) P. Colgan, pp. 43–78. Wiley, New York.

METZ, J., DIENSKE, H., DE JONGE, G. & PUTTERS, F. 1983. Continuous time Markov chains as models for animal behaviour. *Bull. math. Biol.* 45: 643–658.

ODEN, N. 1977. Partitioning dependence, in non-stationary behavioural sequences. In: Quantitative methods in the study of animal behaviour. (Ed.) B. Haslet, pp. 203–220. Academic Press, New York.

OSTER, G. & WILSON, E. 1978. Caste and ecology in the social insects. Princeton University Press, Princeton.

SEELEY, T. 1982. Adaptive significance of the age polyethism schedule of honeybee colonies. *Behav. Ecol. Sociobiol.* 11: 287–293.

SLATER, P. 1976. Data collection. In: Quantitative ethology, (Ed.) P. Colgan, pp. 7–24. Wiley, New York.

SOKAL, R. & ROHLF, F. 1981. Biometry. Freeman, San Francisco.

VAN DER BERCKEN, J. & COOLS, A. 1980. Information-statistical analysis of factors determining ongoing behaviour and social interaction in Java monkeys (*Macaca fascicularis*). *Anim. Behav.* 28: 189–200.

VAN DER HEIJDEN, P. 1986. Transition matrices, model fitting, and correspondence analysis. In: Data analysis and informatics IV. (Ed.) E. Diday, pp. 221–226. North Holland, Amsterdam.

VAN DER HEIJDEN, P., DE VRIES, H. & VAN HOOFF, J. 1990. Correspondence analysis of transition matrices, with special attention to missing entries and asymmetries. *Anim. Behav.* 40: 49–64.

VILLET, M. 1990. Division of labour in the Matabele ant *Megaponera foetens* (Fabr.) (Hymenoptera, Formicidae). *Ethol. Ecol. Evol.* 2: 397–417.

VILLET, M. 1991a. Definitions of 'caste' in social insects. *Ethol. Ecol. Evol.* in press.

VILLET, M. 1991b. Social differentiation and division of labour in the queenless ant *Platythyrea schultzei* Forel (Hymenoptera: Formicidae). *Trop. Zool.* 4: 13–29.

WALKER, J. & STAMPS, J. 1986. A test of optimal caste ratio theory using the ant *Camponotus (Colobopsis) impressus*. *Ecology* 67: 1052–1062.

WILSON, E. 1980. Caste and division of labour in leaf-cutter ants (Hymenoptera: Formicidae: *Atta*). I. The overall pattern in *A. sexdens*. *Behav. Ecol. Sociobiol.* 7: 143–156.

WILSON, E. 1984. The relation between caste ratios and division of labour in the ant genus *Pheidole* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 16: 89–98.