1989

Analyzing The Organization Of Animal Behavior: The Application Of Nonsymmetric Multidimensional Scaling Techniques

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ANALYZING THE ORGANIZATION OF ANIMAL BEHAVIOR: THE APPLICATION OF NON-SYMMETRIC MULTIDIMENSIONAL SCALING TECHNIQUES

by

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Submitted in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy

Faculty of Graduate Studies

The University of Western Ontario

London, Ontario

November 1988

ISBN 0-315-49345-3

ABSTRACT

Several multidimensional quantitative approaches have been applied to the analysis of the organization of behavior. These include chi square, lag saquence analysis, and non-symmetric multidimensional scaling techniques. Transition matrices are generally asymmetric and this is a problematic feature for the first two techniques noted above. Hence it is argued that non-symmetric multidimensional scaling (MDS) techniques are the most appropriate for the analysis of such data sets.

To illustrate these three techniques and to evaluate non-symmetric MDS as a valuable new tool which has been underutilized by ethologists, observational data were collected in a focal animal study of two members of a captive family of meerkats (Suricata suricatta). The results of chi square analyses showed that meerkat behavior could be divided into three major groups -- Solitary Behavior, Active Interactions and Passive Interactions. The patterns of relationship between these major groups of activities, were ascertained using a non-symmetric MDS program called DEDICOM. Solitary activities could be grouped into subclasses labeled foraging, self maintenance and reconnaissance. Clear patterns of transition between these smaller units were identified using MDS DEDICOM. Also

solitary activities are more likely to be followed by Passive Interactions than Active ones. Active Interactions are highly likely to change into Passive Interactions before they are terminated. Lag sequence analyses identified clusters of activities similar to those found using the other two analytical approaches.

Of the three techniques applied, lag sequence analysis was the most difficult to apply and interpret. The chi square analyses produced informative results but still required a degree of subjective analysis. MDS DEDICOM provided clear information both about the clustering of activities into related classes and the patterns of transition between these subgroups. It was concluded that non-symmetric MDS techniques offer the best alternative for the analysis of behavioural organization when the data set to be analyzed is an asymmetric matrix. The simplicity and appropriateness of this technique makes it an extremely valuable tool for the student of behavioural organization.

ACKNOWLEDGEMENTS

SPECIAL THANKS TO

GREG MORAN

MARY GILBERT AND PHIL KRAEMER

BILL ROBERTS AND DAVE PEDERSON

RICHARD HARSHMAN AND PETER OSSENKOPP

JACK DUNNING

MARG LUNDY

PATRICK COLGAN

IDA AND ROSS HUNTER

AND

MUTT

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INTRODUCTION

> ...our conception of science now, towards the end of the twentieth century, has changed radically. Now we see science as a description and explanation of the underlying structure of nature; and words like structure, pattern, plan, arrangement, architecture constantly occur in every description that we try to make. (Bronowski, 1973, p. 68)

Since Wiepkema (1961) first applied factor analysis to fish behavior, the use of multivariate mathematical techniques has become increasingly common in ethology. Yet, as recently as 1978, ethology was described as "still only on the threshold of utilization of quantitative methods in behaviour analysis" (Dunham in Colgan, 1978, p. vii). The reasons for this slowness of ethologists to adopt these quantitative tools are likely twofold -- one a lack of familiarity with the available techniques and, two, a lack of appropriate statistical methods. The purpose of this thesis is to describe techniques appropriate for the analysis of the organization of behavior. One of these approaches, chi square, has been used extensively in the analysis of animal behavior structure. Another, lag sequence analysis has been developed and applied recently while non-symmetric multidimensional scaling (MDS) techniques have had very limited use in the field of ethology. For each of these techniques a brief description will be given, the limiting assumptions will be reviewed, issues in the interpretation of the results will be raised, and an example given. These three methods will then be applied to a data set collected from an ethological study of a social carnivore, the meerkat. It is expected that the MDS technique, while not readily available, will prove to be the most straightforward to apply, and will provide not only the customary groupings of activities but additional information about their structural relationships. In addition, once three dimensional versions of this program become available, they may prove to be the single most powerful tool th~ student of the organization of behavior has at hand. Ethologists struggling with quantitative methodologies will surely applaud this parsimony of mathematical necessity.

At present there is a great deal of controversy and confusion about how to go about understanding the workings of the immensely complex machinery of behavior (Dawkins, 1986). At one end of the continuum is the neurophysiologist who takes a direct approach to mapping the nervous system in order to understand how it gives rise to behavior. At the other end of the spectrum is the ethologist who is essentially working with an "initially mysterious object which is not to be opened but whose workings can be deduced from what it is capable of doing" (Dawkins, 1986, p. 91). In addition, there are several types of combined approaches which fall in between these two extremes.

What is of interest here, is not the particular question of which approach to take to the problem of understanding the 'machinery of behavior', but rather of what tools to use once a particular approach has been adopted. If one chooses the approaches of the neurophysiologist, the tools are well-defined. They include all of the techniques of aseptic surgery and a complement of sophisticated and precise recording devices such as oscilloscopes, electroencephalograms, electromyograms, and a wide range of other accessories. For the ethologist, on the other hand, behavioral taxonomies may be quantitatively analyzed using any one of a variety of unidimensional and multidimensional statistical techniques. The goals of the researchers applying these techniques have been as varied as the techniques themselves, to the extent that to the uninitiated it seems as if there is a unique and idiosyncratic method preferred by each investigator.

The quantitative techniques available to the ethologist range from the use of relatively simple nonparametric statistics such as chi square to the complexities of information theory, multidimensional scaling (MDS), principal components analysis, and factor analysis. This diversity is determined by the goals of the research, the nature of the data set, and the inherent limitations of the different analytical techniques. Only a very few of these techniques are appropriate for an investigation of the organization of activity. Thus the choice of research question is the first point of selection among analytical techniques. Having made this selection, the nature of the data set further limits the choice. Most often the data set is a matrix of frequencies for the observed activities. Three typical matrices are described below. Only one of these is appropriate for analysis using traditional 'spatial' techniques. The other two require special consideration. More on this below.

Traditionally, the ethologist begins by making a lengthy series of careful observations often using cameras and other recording devices to assist in the data collection (see, for example Hinde, 1970; Martin & Bateson, 1986; Sackett, 1978; Slater, 1978). Then these observations are summarized, using one of several sampling techniques, generally on a checklist of one kind or another (see Hinde, 1973). At this point the data are quantified, that is they now become numerical statements of intensity, location, frequency and/or duration for each activity of interest. Investigations of the temporal organization of behavior typically begin with a description of the frequency with which each behavior follows each other behavior in the stream of activity. These frequencies of transition are organized into a matrix or contingency table generally referred to as a transition matrix. One of three types of matrix is generally used. If a comparison among individuals is important, the rows of the matrix may represent individuals while the columns represent activities. The numbers within the body of the table represent the frequency of each activity for each animal. This matrix is similar to the persons by variables table utilized in factor analyses. On the other hand, the matrix might represent the activities of only a single individual. Thus both rows and columns represent activities and the numbers within the table show the frequency with which each activity follows each other activity in the behavior repertoire of a single organism. Finally, a sociometric matrix can be developed in which activities form the headings for both rows and columns as described above, but the rows and columns represent different individuals. The table now represents an action-reaction matrix of transitions. It summarizes the frequencies of reactions by one animal to actions of another. These last two types of matrix are not suitable for typical factor analysis since they are not based on traditional distance metrics.

The question then is, how does one analyze such matrices? There are four major approaches which can be organized into a two-by-two classification. Such a classification is shown in Table 1. The organizing principle on the column aspect is the nature of the items being classified. If one is classifying tangible objects or "things in the world" then a clustering technique is appropriate. If, however, the investigation is to uncover latent attributes, then factor structure models are appropriate. An example of each of the possible techniques is included in the body of the table. In the upper row are the spatial techniques. These are based on commonly understood metrics such as distance or similarity. On the left are the mapping techniques that we are all familiar with. Cities which are separated by short distances will cluster together when mapped. Likewise, persons who share similar characteristics, say attitudes, will be grouped together by factor analytic or MDS techniques. Factor analytic techniques are typically applied to profile data or cross-products data while MDS techniques are used for similarity or proximity data.

Shown in the lower row of the matrix are the non-spatial techniques. These methods are appropriate for data sets which are not based on the typical distance metrics. Unlike

Table 1. How to analyze data matrices to uncover behavioral structure.

	CLUSTERS A TAXONOMY OF "THINGS IN THE WORLD"	OR	DIMENSIONS A TAXONOMY OF "ATTRIBUTES" OR "LATENT FACTORS"
SPATIAL TECHNIQUES	1. MAPPING		1. FACTOR ANALYSIS -for profile data or cross-products data 2. PRINCIPAL COMPONENTS ANALYSIS 3. MDS (PARAFAC) -(Harshman, 1970) -for similarity or proximity data
NON-SPATIAL TECHNIQUES	1. CHI SQUARE 2. LAG SEQUENCE ANALYSIS -(Sackett, 1978,1979)		1. MDS (DEDICOM) -(Harshman, 1978a,b) -for asymmetric or skew-symmetric data

the spatial techniques, these methods do not require that the "distance" from point A to point B be the same as the "distance" from B to A. It is this attribute that makes them especially valuable in the investigation of behavioral structure since the frequency with which behavior A follows behavior B may not be the same as the reverse arrangement. The techniques shown here are chi square and lag sequence analysis for clustering and MDS DEDICOM for uncovering the latent structure of non-symmetric data matrices. These two classes of approach have rather different uses for the ethologist. It appears that the techniques on the left answer the "how" questions. That is, how is behavior organized. The techniques on the right may provide insight into why the behavior is organized that way. In the animal behavior literature this is the approach typically taken by investigators of motivational and evolutionary factors. Applying both types of approaches may offer complementary views of the organization of behavior. The three methods suggested opposite non-spatial techniques are reviewed below. For each technique, the assumptions and limitations are reviewed and an example is given.

Chi Square

Transition matrices such as those described above are typically analyzed using chi square statistics to identify transitions which occur at above chance levels. Chi square is a statistical technique for analyzing the distribution of persons or events among any number of mutually exclusive categories (Spence, Cotton, Underwood & Duncan, 1983). The hypothesis tested is that the classification of events or individuals according to one property is unrelated to their classification according to another property (a test of independence). To test the null hypothesis that the groups were drawn from the same (dependent) population, the observed distribution of items is compared to theoretically expected frequencies. The expected frequencies generally are derived using an equal-likelihood model, however, chi square can be used to test any _a priori_ hypothesis. If the deviations between observed and expected values are statistically significant, one can conclude that a nonchance factor was operating to determine the observed distribution.

Like any statistical method, the use of chi square is subject to certain limitations. There are five such restrictions on the use of chi square. First, it can be used only with frequency data. Second, the individual events or observations must be independent of each other. This may be problematic in the investigation of behavior since successive responses by the same individual are probably not independent. Third, no theoretical (expected) frequency should be smaller than 5. This rule may be relaxed if the contingency table has more than 4 cells and only 'a few' of the expected frequencies are less than 5 (Howell, 1987). Here there are potential problems when a large number of behavioral acts are recorded but some occur rarely or an insufficient number of observations has been made. Fourth, there must be some basis for the way the data are categorized. The categories must be defined beforehand, and it must be demonstrated that they are reliable. The ethological literature offers many useful guidelines in this regard (see, for example, Bakeman & Gottman, 1986; Hinde, 1970; Martin & Bateson, 1986; Slater, 1978). Finally, the sum of the observed and the sum of the expected frequencies must be the same. Related to this last point is the fact that the data must include both the frequency of occurrence and the frequency of nonoccurrence. It is not always clear what nonoccurrence is in a traditional transition matrix. As an additional consideration, frequencies of transition from an activity to itself often are not described hence the diagonal of the matrix contains logical zeros. This also disrupts the independence structure in the matrix and the analysis must be modified accordingly (Castellan, 1979; Colgan & Smith, 1978; Goodman 1968, 1984).

When the overall chi-square for any matrix is significant, post-hoc tests to evaluate particular cells in the matrix are of interest. There are no generally accepted criteria for determining how many transitions to include when there are many significant ones. Fagen (Fagen, 1978; Fagen & Young, 1978) recommends that the individual cell values be evaluated against the appropriate chi-square critical value corrected for the number of cells in the matrix. This formula often results in many significant individual transitions. The most conservative approach involves choosing a critical value for alpha and 1 degree of freedom and assuming a repertoire size of 1. Either way, the resulting transitions from cell _i_ to cell _j_ that are significant and positive indicate that activity _j_ follows activity _i_ with a frequency that is significantly higher than a random model would predict. Transitions from _i_ to _j_ that are significant and negative indicate that activity _i_ in some way significantly inhibits the occurrence of activity _j_. The results of these _post hoc_ analyses often are presented visually as flow diagrams showing those transitions which occurred significantly more or less often than expected (see, for example, Morgan, Simpson, Hanby & Hall-Craggs, 1975). An example of the application of chi square to the analysis of behavior structure follows.

Meerkats are members of the family of smelly carnivores (see, for example, Gorman, 1980) and they scent mark regularly (Moran & Sorensen, 1986, Sorensen, 1981). Scent marks were most often deposited by lifting one hind leg and the tail, raising the hindquarters, and then wiping the anal pouch along a vertical surface with a downward motion of the supporting leg and torso. Body rubs along the object to be scent marked, and sniffs and scratches also directed at it often occurred in conjunction with these leg lifts. In order to examine the patterning of these activities, both in sequences that included leg lifts and sequences that did not, over 200 instances of each type of sequence were recorded and then analyzed using the chi square statistic (Moran & Sorensen, 1986). In both cases the observed transition matrix was significantly different from a random distribution. Flow diagrams were then created showing the most significant transitions. These flow diagrams gave a clear picture of the relationship between the activities of interest (for details, see Moran & Sorensen, 1986). In this way, the arrangement of activities related to scent marking was described for the species.

There is no question that chi square techniques have proven valuable in the analysis of the organization of behavior. However, there remain a number of limitations that must be kept in mind in their application. It is important that the assumptions underlying the analysis of cross-classified data, as reviewed above, be kept in mind, and it is important that the sample size be adequate. Also, thoughtful decisions must be made about treatment of the entries on the diagonal of the matrix and with the choice of significance levels. Finally, care must be exercised in the choice of visual arrangement and interpretation of the significant transitions. With these considerations in mind, chi square techniques can continue to offer the ethologist a tool for "mapping" the organization of behavior.

Lag Dependencies.

Lag sequence analysis is a valuable approach to discovering the patterns of organization for activities that are not immediately adjacent in the stream of behavior. Lag sequence analysis is based on the multinomial distribution in which each of a number of independent trials results in one of several mutually exclusive outcomes. (Note that when the number of possible outcomes is limited to two, the general multinomial distribution becomes the more familiar binomial distribution.) The binomial distribution is an integral part of chi square analyses and thus lag sequence analysis is closely related to the chi square technique described above. As for chi square, having an adequate sample size is critically important. Neither the binomial nor the multinomial produce anywhere near normal distributions for small sample sizes and for small expected frequencies. However, despite these considerations, lag sequence analysis offers a type of information about the arrangement of activities that has hitherto been unavailable.

The majority of ethological studies that have analyzed the contingencies between events have restricted themselves to immediately adjacent lag 1 transitions (see for example Hazlett & Bossert, 1965; Moran & Sorensen, 1986; Rasa, 1977, 1984; van Hooff, 1970, 1973; Wiepkema, 1961). Lag sequence analysis (Sackett, 1978, 1979) is an alternative way of looking at the serial dependencies among behavior elements. Such an analysis identifies significant dependencies which may exist between behavior elements which do not occur immediately adjacent to each other. Such dependencies, beyond lag 1, would not emerge from chi square analyses of the typical transition matrices described above.

A lag is defined as the number of event (or time unit) steps between sequential events. Thus a transition matrix is formed based on the frequency of transition from one event to another at a predetermined number of event units or time units later. Lag sequence analysis measures the probability that behavior patterns of interest precede or follow a criterion behavior at various lag steps in the ordered data. The results indicate behavior sequences at particular lags with significantly increased or decreased probabilities of occurrence.

Sackett (1979) analyzed data for crab-eating monkey mother-infant interactions. He recorded one of nine behaviors whenever a change in the activity of either the mother or infant occurred. In this investigation, Sackett used the lag sequence approach to identify contingent relationships among large numbers of behaviors which might persist through a period of time or over a number of events (lags). Sackett found evidence for significant lag dependencies up to event lag 9. He also found that some events were inhibited (their probabilities of occurrence decreased) or facilitated following criterion events. From these results Sackett was able to identify 3- and 4-step chains of behavior that occurred with a relatively high frequency.

Since lag sequence analysis is essentially an analysis of binomial probabilities, the assumptions that must be kept in mind are that sample sizes and binomial (or multinomial) probabilities must be large enough. The question of how large has yet to be resolved in the statistical literature. Sackett uses the guidelines that the total frequency with which one activity occurs following all others (the column totals in the usual transition matrix) must be at least 30 and the expected frequency should be at least five. These appear to be relatively conservative figures (Howell, 1987). In short, the limitations on lag sequence analysis are identical to those for the chi square technique reviewed above -- failure of the assumptions and large sample size.

Factor Analysis and Multidimensional Scaling.

Factor structure models such as factor analysis and MDS are two additional approaches to the reduction of transition matrices into subsets of categories which are based on temporal associations. These models are applied to data sets when some latent variate or unknown factor such as motivation is assumed to underly specific sequences of behavior. A small number of latent factor variates is derived that represents the observed variates. These groupings are then interpreted using motivational, functional or evolutionary concepts.

There are several problems with applying factor analytic approaches. The problems of determining dimensionality, communality, and indeterminacies of scale and rotation apply to all types of data matrices, while intrinsic asymmetry is a troublesome characteristic of contingency tables. Each of these problems is reviewed briefly. The problems and potential solutions raised below are common to all types of principal components, factor analysis and multidimensional scaling techniques.

No natural criteria exist for deciding when a sufficient proportion of the variance has been accounted for by the principal components or the derived factors (Morrison, 1967). This is the problem of determining dimensionality or the number of factors or categories which adequately represent the raw data. Those applying factor analytic techniques typically continue looking for latent factors until some major proportion of the variance (e.g. 80%) has been accounted for. Recently at least two additional approaches have been suggested. Kruskal and Wish (1978) recommend a measure called stress which indicates how well the derived matrix represents the data. Low values on this measure represent a good "fit" between the estimate of the data matrix based on the factor solution and the data matrix itself. Stress is computed for each successive factor solution (i.e. beginning with one factor and incrementing step-wise). Stress will start out high and decrease with each additional factor. A point will be reached at which each additional factor fits only a small additional part of the variance and the stress value will decrease only minimally. It is reasonable to assume at this point that the additional variance being fitted is error variance. When the stress values are plotted, a sharp "elbow" will be noticeable at this point. The point at which the elbow occurs indicates the factor model which should be accepted.

Harshman (Harshman, 1978a, 1978b; Harshman, Green, Wind, & Lundy, 1982) describes a similar procedure based on the correlation between the derived factor matrix and the raw data matrix. The correlation will increase with each additional factor. If the square of this correlation (the coefficient of determination) is plotted, the resulting fit-dimensionality curve will show the proportion of variance accounted for and will also have an elbow at the point where additional factors begin to fit error variance. Each of these methods offers an objective criterion for when to stop factoring. Once the optimum number of factors is determined, it is this solution that must be interpreted.

Sometimes the values on the diagonal of a data matrix are logical zero's. Even if these are non-zero values, as in an action-reaction matrix, it is often logical to assume that they have different underlying motivational or causal bases than the remaining entries in the matrix. This problem is referred to as communality in the factor analysis literature. (In a correlation or covariance matrix this is not a problem since each of these entries will be 1.) In the analysis of a contingency matrix, it may be best to ignore the actual values on the major diagonal and estimate them from the data (Goodman, 1968, 1984; Harshman, 1978a, 1978b). In this way they will be based on the same underlying factors as the rest of the matrix.

The next consideration for all factor analytic approaches is to decide whether to do the analysis in the original units of the responses or to transform each cell entry in the data matrix. Some authors recommend that all scores be transformed into proportions (e.g. Spence, 1978 recommends transforming the data matrix so that all rows and columns total 100 making individual cell entries proportions). If the responses are reasonably commensurable, the covariance form has the greatest statistical appeal (Morrison, 1967). Standard scores are useful if the responses are measured in widely different units (Harshman, 1970; Harshman & Berenbaum, 1981). For example, heart rate and lung capacity might both be used in an assessment of cardiovascular fitness yet they are not measured in directly comparable units. Such preprocessing can also be applied to data such as scale data to remove the effects of additive constants which are likely to arise when each response item does not have a natural origin of zero.

Rotational indeterminacy is another thorny problem. Investigators may use graphical or analytical rotation techniques to obtain "simple structure". Varimax or orthogonal rotations provide factors that are maximally distinct or independent of each other. Oblique rotations, on the other hand, permit individual variates to influence more than one factor resulting in "fuzzy" clusters. Often an *a priori* decision can be made, based on the nature of the data, as to whether independent or fuzzy clusters are appropriate. *A posteriori* criteria include parsimony, ease of interpretation, and the degree to which the derived factors represent reality as understood by the investigator.

An additional difficulty arises in the application of factor analysis to behavioral transition data. Transforming the transition matrix into a correlation or covariance matrix, necessary for factor analysis, may obscure interesting information. For example, in a frequency table, behavior *i* might follow behavior *j* with a very high frequency but the reverse might happen only rarely. As a consequence the *ij* cell in the matrix and the *ji* cell would be unequal and the matrix could be described as asymmetric or skewed. Such asymmetry does not exist in correlation matrices and in the past has been treated as a nuisance in transition matrices and deleted (Harshman, 1978a; Harshman et al., 1982; Rasa, 1977b; Wiepkema 1961). When the intrinsic asymmetries are considered to be of interest, such an approach is inappropriate. Non-symmetric MDS techniques are specifically designed to deal with such asymmetries.

Recently Harshman (1978a,b; Harshman et al., 1982) has developed a non-symmetric MDS technique which permits an investigation of not only the latent factor structure of a data matrix but also the asymmetries in the data. His approach, called DEDICOM (DEcomposition into DIrectional COMponents), allows for the input of an asymmetric matrix and outputs the familiar factor loadings <u>and</u> a matrix showing the relationship between these factors. This relationship matrix can be understood as a higher-order transition matrix. Non-symmetric MDS techniques such as DEDICOM represent a tremendous advance over traditional factor analytic techniques for such data matrices. A recent report is illustrative. In an investigation of consumer activity, Harshman and his colleagues (Harshman et al., 1982) applied the DEDICOM model to brand switching data obtained in two marketing research studies. They concluded that these DEDICOM solutions made more substantive sense and provided a better fit with the asymmetric data sets obtained than solutions obtained using traditional factor analysis or MDS techniques. They also found the relations between the dimensions or clusters, information that is not available using other factor analytic techniques, to have useful marketing implications. This methodology has not been applied to the investigation of the organization of animal behavior (but, see Spence (1978) for a reanalysis of data from an earlier ethological study using the non-metric option of another MDS program).

In short, when used in conjunction with a stress-like measure, and thoughtful decisions about rotation and transformation of the raw data, non-symmetric multidimensional scaling techniques may prove to be the best alternative for analyzing the asymmetric transition matrices typical in investigations of behavioral structure. One limiting factor is that, at present, the program will accommodate a maximum 30 X 30 matrix.

<u>Summary</u>

Of interest in this thesis are methodological approaches that are appropriate for the analysis of the structuring of sequences of activities. The range of available quantitative techniques is severely restricted. Multidimensional scaling techniques, especially nonmetric ones, are particularly valuable for analyzing behavioral structure because they minimize the number of limiting assumptions and accommodate asymmetric or skewed matrices. In addition, in the case of the particular application used (DEDICOM), additional relationships between the dimensions of the data set become available. Like other geometric models, DEDICOM will reduce the dimensionality of a multivariate data set and thus identify the 'main patterns' in the behavioral repertoire of the study species and may provide a solid base from which to generate further research ideas and hypotheses. What DEDICOM provides that other quantitative techniques have not is the relationship between the dimensions. This additional information is a tremendous advance over earlier methods for analyzing behavioral structure and is particularly exciting for the student of the patterns and regularities in behavior structure. Once three dimensional MDS techniques become available (in development; Harshman, personal communication), this single tool will be able to accomplish much of what ethologists have been doing with chi square, factor analysis, and lag sequence analysis. The advantage of having to learn only a single quantitative technique is obvious and this should have tremendous appeal to ethologists.

The non-spatial techniques described above will be applied to data collected in an ethological study of the meerkat (Suricata suricatta). This will represent one of the first applications of non-symmetric MDS techniques in the ethological literature. The application of these techniques will permit statements about the organizational patterns of meerkat behavior. In addition it will be possible to uncover the latent factor structure. These factors will be labeled and interpreted in the traditional ethological manner using motivational, functional and evolutionary concepts.

Chapter II

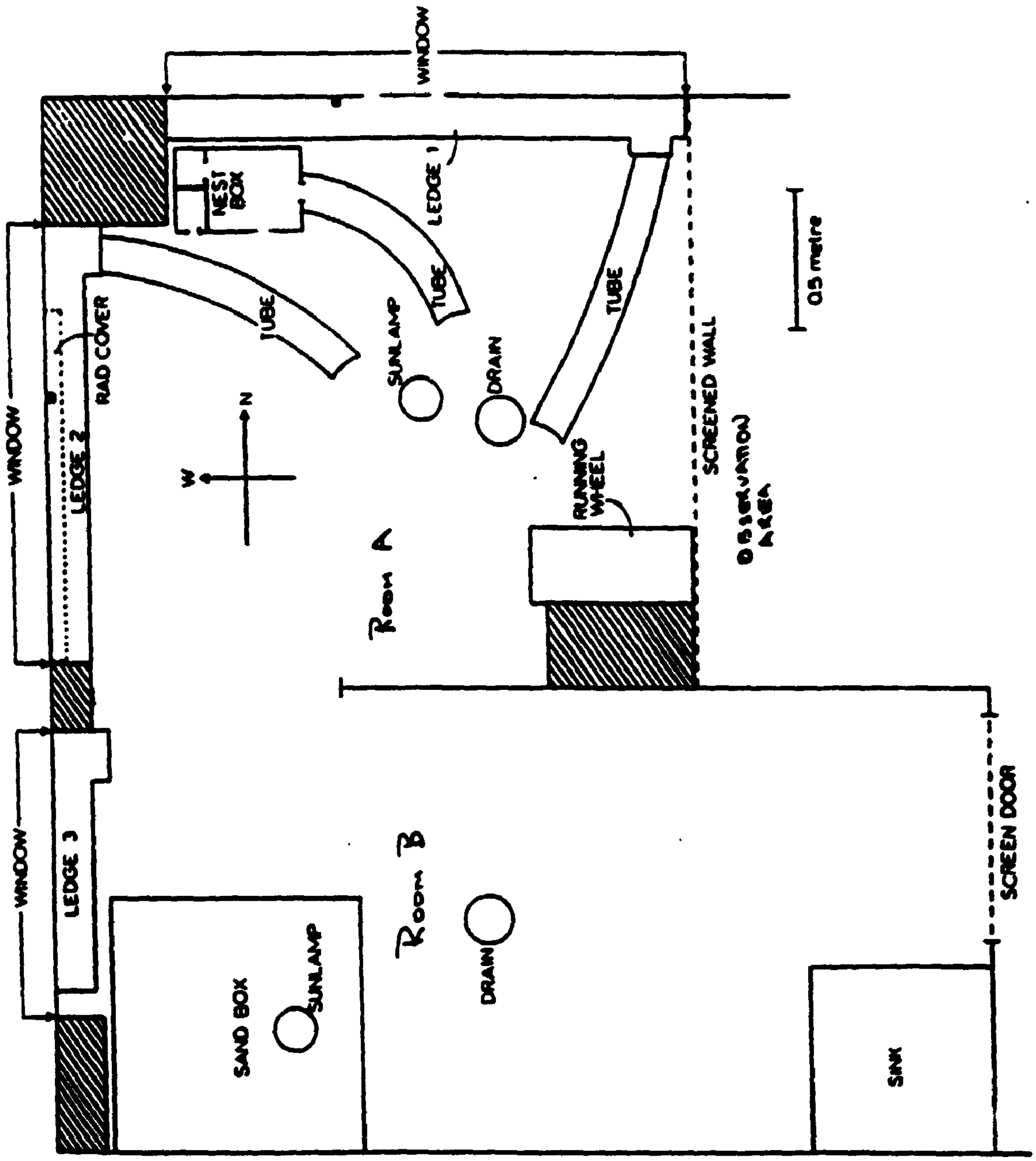
METHOD

Subjects and Housing

Two meerkats (one male-- Charles, and one female--Diana) were born in September 1982 into a captive family consisting of a mated pair and two male offspring. The mated pair, XII and Karen, were each four years old when Charles and Diana were born. Hazel and Filbert were born to the same pair of adults in April 1981. Hazel and Filbert are referred to as juveniles and Charles and Diana as infants throughout the study for convenience. All animals were born in captivity. The meerkats were fed a meat-based diet supplemented with fresh fruits and vegetables and a vitamin-mineral supplement formulated by the nutritionist at the Metropolitan Toronto Zoo.

This family was maintained in the enclosure shown in Figure 1. Three large windows in the enclosure provided natural light. The room lights were automatically turned on at 8:00 a.m. each day and off at 8:00 p.m. The thermostat in the enclosure was maintained at a constant setting of 25 degrees celsius. The room was designed to accommodate the full behavior repertoire of the species. Plastic tubing and nest boxes were provided to simulate underground burrows. A sand box was included to allow for digging and for elimination. Access to the window ledges was provided via

Figure 1. The enclosure. Animals were confined to Room A during filming sessions. Access to the window ledges was via the tubes and wooden ramps.


WINDOW
LEDGE 1
NEST BOX
TUBE
TUBE
TUBE
0.5 metre
SUNLAMP
DRAIN
RAD COVER
WINDOW
LEDGE 2
N
W
SCREENED WALL
RUNNING WHEEL
OBSERVATION AREA
Room A
WINDOW
LEDGE 3
SCREEN DOOR
Room B
SAND BOX
SUNLAMP
DRAIN
SINK

wooden ramps and lengths of plastic tubing. An exercise wheel was also available as were two sunlamps for warmth.

Maintenance of the enclosure was undertaken early each day, well before the filming sessions. Animals were filmed in the early afternoon and food and water bowls were present continuously. Food was replenished once each day following the filming session.

Apparatus

A Panasonic colour video camera (model WV 3890) was used with a video counter timer (Tel Video Products) and a Panasonic Video Cassette Recorder (VHS format) model NV-8950. Tapes were analyzed using a Panasonic colour video monitor (CT-110MCA).

Observation Protocols

During the first four weeks after the birth, the young animals spent most of their time in the nestbox. After this initial period, each of the infants was videotaped using a focal animal technique in which the camera was focused on the target animal for the entire filming session. The other members of the group were filmed only if involved in an interaction with the focal animal. Each animal was filmed for 15 minutes, twice each week, at approximately 2:30 pm for Weeks 5 through 52. (There are four exceptions: Each animal was filmed once during Weeks 5, 22 and 27 and three times during Week 11. This resulted in a total of 188 film sessions.) The animal filmed first each day alternated on a random basis. All animals in the group were confined to Room A (see Figure 1) for at least 15 minutes prior to each session and throughout the filming. The observer always stood at the observation area with the videotape equipment behind her.

All filming sessions were analyzed by a single observer using the 32 behavior codes described below. Behavior emitted by the focal animal as well as behavior directed toward it by any other family member was recorded. An all-event sampling method (Hinde, 1970) was used. During film analysis, the initiator, action code, and object (inanimate or other animal as appropriate) were noted for each behavior that occurred. Elapsed time, generated by the video counter timer at the time of filming, was noted with each action recorded. The data recorded for Charles on 30 May 1983 are included as an illustration in Appendix A. During the data analysis process, urination and defecation, originally recorded as part of the scent marking complex, were coded as distinct activities. As a result, a total of 34 action codes were recorded.

Behavior Codes

The following activities were defined prior to the study and were used throughout. Capsule definitions are included.

ACTION CODE	OBJECT	DESCRIPTION
10 EAT	1 Purina Cat Chow/ Romar 90 Dog Food	The usual definition.
	2 Fruit/ Vegetables	
11 DRINK	1 Water	The usual definition.
	2 Other (Urine)	
12 CARRY	1 Food 2 Other	Any instance of carrying an item in the mouth from one location to another.
13 SELF GROOM	1 Feet, Legs, or Tail 2 Ventral Surface or Genitals 3 Back or Sides 4 Wipe Face 5 Scratch self	Animals generally used the teeth or tongue to groom the pelage. Brief wipes were occasionally made at the face or teeth with the paws or claws of the front feet. Sides were occasionally scratched using a hind foot.

14 LOCOMOTE and 15 RUN	1 On Floor	Normal quadruped locomotion around the enclosure at either a regular rate or a fast pace.
	2 Plus Sniffing	
	3 On Radiator	
	4 On Ledge	
	5 On Nestbox	
	6 Jump Up	
16 IMMOBILE POSTURES	1 Alert Stand (Rear)	Hind legs fully extended with the tail for support.
	2 Alert Sit	Hind legs relaxed, back straight, and forefeet off of the ground.
	3 Lazy Sit	Hind legs and lower back relaxed with the forefeet off the ground.
	4 Lazy Fours	Hind legs and lower back relaxed with the forefeet supporting some weight.
	5 All Fours	Normal quadruped stance.
	6 Stretch & Yawn	The usual definition.
	7 Body Shake	Full body shake.
	8 Head Shake	Shake limited to head.
	9 Sniffing	Any immobile posture accompanied by sniffing.

17	LYING DOWN	1 On Back 2 Stomach 3 Side	Legs relaxed, often fully extended with the weight on the trunk of the body.
18	SCRATCH/DIG	1 Tubes 2 Door 3 Food 4 Other	Use of the forefeet to scratch at items in the enclosure except at known scent marks.
19	LEDGE	1 Up-Left 2 Up-Right 3 Head in Tube 4 Down	Used to signify the start, end and location of a period of time on a window ledge. See Figure 1.
20	NESTBOX	1 Head in Tubes 2 Right (Large) 3 Left (Small)	Head in the nestbox tubes. An animal was considered to be in the nestbox once all four feet were in the nestbox tube.
21	SCENT MARK AN OBJECT	1 Defecate	The usual definition.
		2 Urinate	The usual definition.
		3 Perineal Drag	Dragging the perineal area across an object in a squatting position.
		4 Rub	Rub the body from shoulder to flank along an established

marking post.

5 Sniff	Sniff at a known scent mark.
6 Scratch	Scratch at a known scent mark.
7 Leg Lift	Scent marking an object with the anal scent gland. While in a standing position, one leg is raised and the tail averted while the anal area is lowered down a vertical surface.
8 Sniff+Lift	
9 Sniff+Scratch+Lift	

BEHAVIOR ELEMENTS 22 TO 41 EACH HAVE
ANOTHER ANIMAL AS THE OBJECT

22 SNIFF	Sniffing the pelage.
23 PAW	Pawing the pelage.
24 WALK OVER	One animal walks over another animal. Occurs most often on narrow ledges or tight corners.
25 STAND OVER	Standing immobile over another animal without other apparent interaction.
26 REST IN CONTACT	Passive contact with one or more family members.

27 BITE	Contact between the teeth of one animal and the pelage or body part of another. Often accompanied by head shaking.
28 SCENT MARK	Allomark.
29 GROOM	Allogroom.
30 MUTUAL GROOM	Reciprocated grooming.
31 LATERAL PUSH/HIP SLAM	Generally accompanied by rasping vocalizations.
32 CLASP FROM ABOVE	Mount.
33 BIPEDAL CLASP	While standing erect on the hind legs, two animals clasp each other with the forelegs.
34 HEAD FENCE	Open-mouthed sparring generally accompanied by the bipedal clasp.
35 POUNCE	While on the hind legs, both forelegs are brought down on another animal with force.
36 CHASE	Running in pursuit.
37 INVESTIGATE GENITALS	Sniffing, pawing, or licking another animal's genital area.
38 HEAD THRUST ("DART")	An abbreviated lunge at another animal which involves only the head; no contact

	between the head of the "darting" animal and the target animal results.
39 LEAVE AN INTERACTION	The identification of the animal(s) leaving an interaction was noted.
40 EN FACE	Similar to an abbreviated "head fence" when animals are separated by one body length or more.
41 COMPETE FOR OBJECT	Generally pawing at a (food) object that another animal is already involved with.

Data Collection and Analysis

The information extracted from the tapes was recorded on data sheets and then transferred to a DECSystem 10 Computer for storage and analysis. Fortran programs were developed to facilitate summarizing and analyzing the data. The Fortran program developed to complete a chi square analysis is included as Appendix B. Additional programs were designed to complete the lag sequence analysis (included as Appendix C). Access to the MDS DEDICOM program was provided through the generosity of R. Harshman.

Reliability

In ethological analyses, the ethogram is designed in such a way as to simplify and standardize the recording process and thus to minimize the element of error in the recordings. Although no direct measure of reliability was employed, there are two aspects of the results (reported in more detail in the following chapter) which indicate that both the recording techniques and the behavior of the animals remained relatively constant over the period of investigation. Significant correlations between the frequency of activities ($r= .9863$, $\underline{p} < .0001$) and for the duration measures ($r= .8551$, $\underline{p} < .0001$) indicate that the activity distribution for each of the two meerkats observed in this study is markedly similar. This suggests that the recording techniques and the behavior of the animals were constant over the recording period. A representative "split half" analysis is also included in the Results section. In this case odd numbered weeks were compared to even numbered weeks and this analysis showed a high degree of constancy over all weeks of the study. This indicates that factors such as random variation in the environment had no significant effects on behavior. Taken together, these two assessments of reliability suggest a high degree of stability in both the behavior of the animals and the recording methods.

Chapter III

RESULTS

Overview

The results of the current study indicate that the frequencies and durations of the activities of these meerkats were stable over the 48-week study period. The three methods of analysis offer insight into the organization of meerkat behavior. There appear to be three major groups of activities. They have been labeled Active and Passive Interactions and Solitary Behavior. The solitary activities cluster around the locomotion and immobile codes. They link to social acts through lying down and ascending one of the window ledges (ledging). This was confirmed by a DEDICOM analysis which showed the social activities clustered together with lying down, running and ledging. The remaining solitary acts arranged themselves into three clusters called Self-Maintenance, Foraging and Reconnaissance.

In a subsequent DEDICOM analysis in which all solitary acts were treated as a single event, the remaining activities clustered into two groups -- Active and Passive Interactions. Each of these activity classes was then analyzed for organization within the clusters. The elements of Active Interactions form two smaller segments, one grouped around head fencing and the other clustered loosely around pawing at another animal. Active Interactions appear to change into Passive Interactions before they terminate (link to Solitary Acts). Passive Interactions include grooming, sniffing and resting in contact which form a single cluster.

The lag sequence analyses show the way in which the probability of occurrence of one activity is determined by the preceding act. For example, locomotion and immobile are facilitated for at least 15 events following scratch/dig. On the other hand, rest in contact is inhibited significantly following scratch/dig through the same number of event lags. The duration of this facilitation/inhibition is variable as shown by the matching probabilities of grooming, pawing, and genital investigation following sniffing another meerkat. Lag sequence analysis is typically used to identify chains of activity that are highly probable. One such chain, which included chase-pounce-head fence, was identified. All other activities showed the clustering evidenced by the earlier analyses.

Frequency and Duration

The frequency and duration for each activity over the entire period of the study is shown separately for Charles and Diana in Table 2. There are apparent similarities

Table 2. Overall frequency and duration measures for Charles and Diana for each of the activities recorded.

	CHARLES		DIANA	
BEHAVIOUR	TOTAL FREQUENCY	TOTAL DURATION (SEC)	TOTAL FREQUENCY	TOTAL DURATION (SEC)
URIN/DEF	12	133	12	174
HEAD-IN-TUBE	183	479	199	635
EAT	262	2443	333	2851
DRINK	65	308	86	414
CARRY	25	68	10	24
SELF GROOM	212	1234	226	1008
LOCOMOTE	2812	7526	2552	6328
RUN	184	317	319	519
IMMOBILE	2027	10910	1927	7815
LIE DOWN	135	2438	121	3553
SCRATCH/DIG	1264	9791	1656	11777
LEDGE	97	15883	94	16071
NESTBOX	76	3829	66	6689
SCENT MARK	210	3613	164	505
PAW	301	671	349	933
WALK OVER	50	91	40	74
STAND OVER	65	197	49	237
BITE	498	1023	647	1332
ALLOMARK	14	22	10	15
LATERAL PUSH	255	939	202	813
CLASP (MOUNT)	165	387	193	477
BIPEDAL CLASP	27	42	33	42
HEAD FENCE	706	1547	718	1479
POUNCE	244	298	387	441
CHASE	109	162	162	255
DART	234	279	314	417
EN FACE	181	270	133	194
COMP FOR OBJ	21	60	29	77
SNIFF	107	308	104	258
REST IN CON	1632	16696	1546	12676
ALLOGROOM	82	478	104	594
MUTUAL GROOM	38	295	40	284
INV GENITALS	62	283	62	361
OUT OF SIGHT	126	1001	130	1286
TOTALS	11481	84021	13017	80608

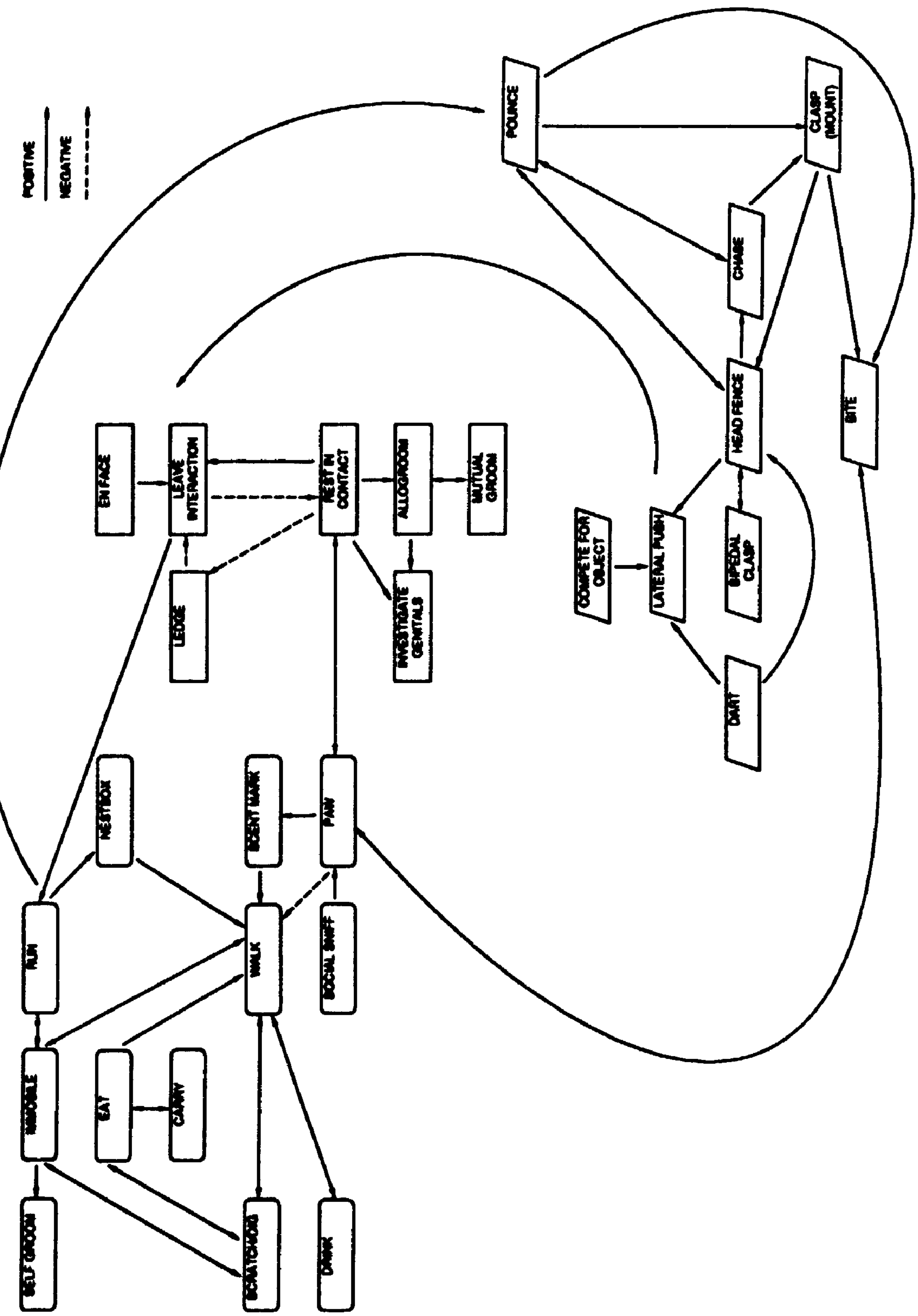
between each of these measures for each activity for these two animals. To test these similarities statistically, Spearman rank order correlations were calculated. For the frequency measures the correlation was .9863 ($p < .0001$) and for the duration measures it was .8551 ($p < .0001$). These correlations suggest that the activity distribution for each of the two meerkats observed in this study is markedly similar. As a consequence, the data have been treated as if they were from a single animal throughout.

The first step in the analysis of behavioral structure was to create a 34 by 34 transition matrix from the raw data. The rows and columns in this matrix represented the 34 activities described earlier (32 plus 2 that were recoded). Each cell in the matrix represents the frequency with which the column behavior followed the row behavior as the next activity. For the solitary activities, behavior was defined in such a way that transitions from an activity to itself would not occur. For the social activities, an action may follow itself but only if the identity of the actor changes as well. Except for the first and last activity in each observation session, all acts served both as the start behavior and the follow behavior. Expected frequencies were calculated and a chi square analysis was completed using the Goodman (1968, 1984) test for quasi-independence. The observed transition matrix was significantly different from a random distribution, χ^2 (1089, $\underline{N}$ = 41156) = 58533.85, $\underline{p}$ < .001.

In order to further investigate the distribution of all activities, the transitions between activities that had individual cell chi square values greater than or equal to 100 (even more conservative than choosing a critical value for degrees of freedom of 1) were plotted in the flow diagram shown in Figure 2. (All of these transitions are significant beyond the .001 level). There were 90 individual cells that met the criterion and together they accounted for 82.3 % of the overall chi square. Activities have been grouped in Figure 2 in such a way as to minimize overlap of the significant lines of transition. Those transitions with observed values greater than expected are shown as positive or facilitatory transitions and those with observed values significantly less than expected are shown as negative transitions. All of the positive transitions are shown and some of the negative transitions are included here also.

There appear to be three main clusters of activities in the flow diagram shown in Figure 2. In the left of the figure are the solitary activities, in the centre are what are subjectively called passive interactions and in the right of the figure are the active interactions. The

Figure 2. A schematic representation of some of the significant positive transitions ($p < .001$) from a chi-square analysis of the full data matrix. The solid lines represent significant positive transitions while the dashed lines indicate significant negative transitions. Negative transitions are included only where they do not obscure the figure (see the text). The items in the upper left corner with the rounded corners on the boxes are interpreted as solitary activities, those in the centre in the square cornered boxes as passive interactions, and those in the angled boxes, in the lower right of the figure, as active interactions.


POSITIVE
NEGATIVE
POUNCE
CLASP (MOUNT)
CHASE
HEAD FENCE
BITE
COMPETE FOR OBJECT
LATERAL PUSH
BIPEDAL CLASP
DART
EN FACE
LEAVE INTERACTION
REST IN CONTACT
ALLOGROOM
MUTUAL GROOM
LEDGE
INVESTIGATE GENITALS
NESTBOX
SCENT MARK
PAW
RUN
WALK
SOCIAL SNIFF
IMMOBILE
EAT
CARRY
SELF GROOM
DRINK

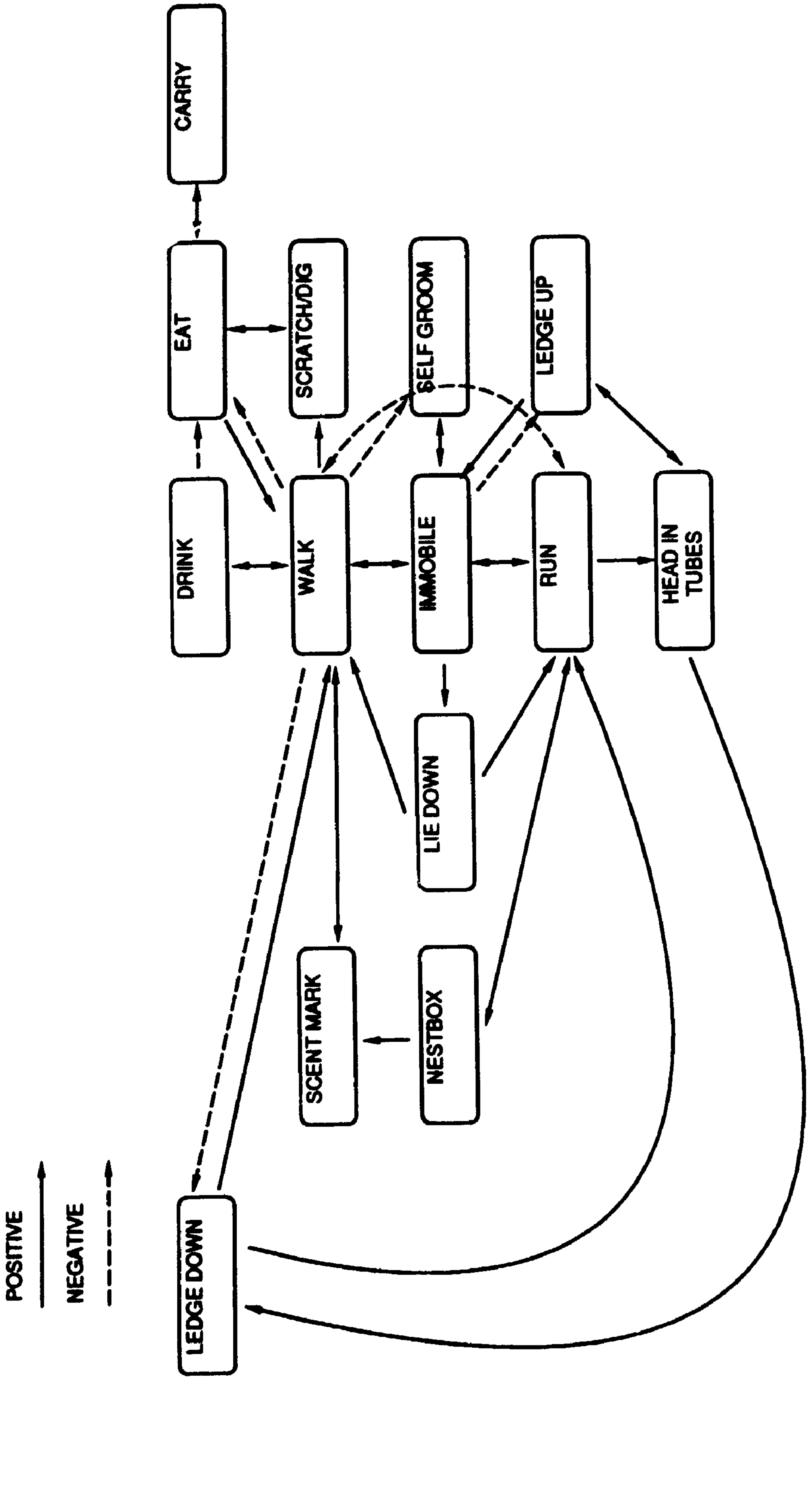
solitary activities include self grooming, eating and drinking, locomotion and scratching and digging at objects in the enc'osure. The passive interactions include resting in contact and allo- and mutual-grooming. Sniffing and pawing at the fur of another meerkat appear to belong to this complex of activities also. The active interactions are characterized by head fencing, clasping, chasing, pouncing and pushing. There is also a hint here about how these "chunks" fit together. Locomotion is linked to scratching/digging and eating as well as to immobile postures while immobility is linked to self grooming. This suggests a connection between the eating complex and the grooming one. In addition, immobility is linked to running and pouncing which is in turn linked to the head fencing complex. The linkages can be extrapolated further to the link between solitary and social activities. Both of the interaction categories appear typically to end with an animal literally running away from it. These results offer considerable information about the patterning of activities as contiguous events. They suggest that meerkat behavior is highly organized and that it can be classified into solitary and social activities.

In addition to the transitions shown in Figure 2, there are 18 significant negative transitions. When included with the positive transitions, they make for a very complex picture. Even when plotted alone, the figure is so complex as to be almost uninterpretable. (This is probably a function of the fact that doing one thing precludes many other activities.) In each case the flow diagram of the negative transitions was far more complex and intertwined than that for the positive transitions. As a consequence, in this and in all subsequent flow diagrams created from the chi square analyses, the significant negative transitions are only included where they do not obscure the transition patterns of the positive transitions.

Within-Individual Organization

A first chi square analysis was completed for the solitary activities only. These are the first 14 activities listed in Table 2. Although the overall chi square was significant indicating that the observed transition matrix was organized in a non-random fashion, [χ^2 (155, N = 15890) = 14047.86, $p < .001$], 45% of the cells in the expected frequency matrix were less than 5. Hence the following interpretations must be considered with caution. Eating, drinking, and carrying an object (always a food object) form a small cluster shown in the upper right corner of Figure 3. They connect to the other solitary activities through normal locomotion (WALK) and scratch/dig (SCR/DIG). It is interesting to note that walking and running are so distinct

Figure 3. Positive transitions ($p < .001$) which resulted from a chi square analysis of the solitary activities only. As in Figure 2, negative transitions are included only where they do not obscure the figure (see the text) and boxes with rounded corners have been utilized. Note that walking and running are connected by a dashed line indicating a significant negative relationship in the transitions between these two activities.

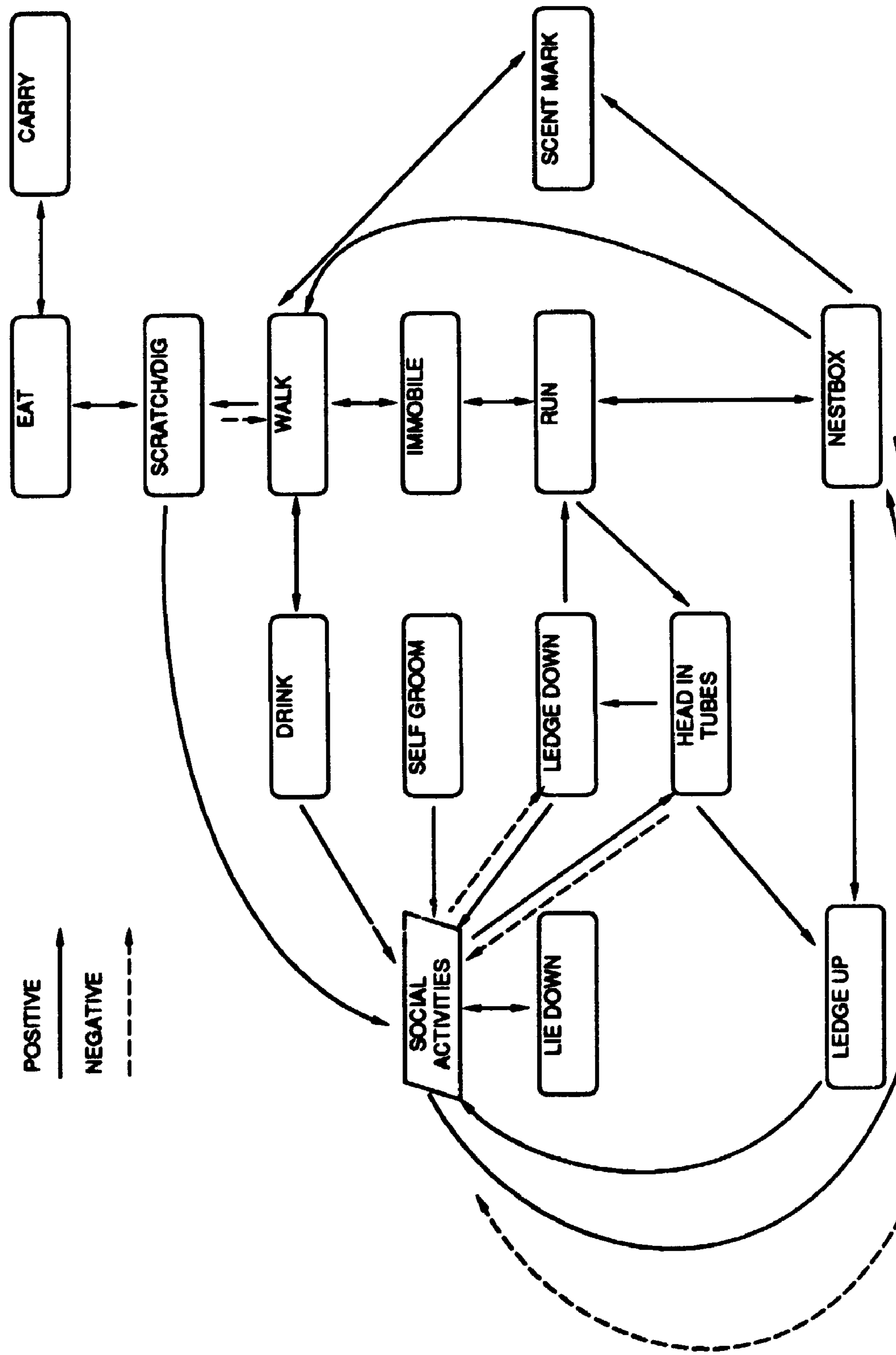

POSITIVE
NEGATIVE
CARRY
EAT
SCRATCH/DIG
SELF GROOM
LEDGE UP
DRINK
WALK
IMMOBILE
RUN
HEAD IN TUBES
LIE DOWN
SCENT MARK
NESTBOX
LEDGE DOWN

in this figure suggesting that they are in fact two separate activities and not gradations of a single one. Self grooming occurs in relative isolation, always after an animal has paused in an immobile stance. It is also of interest that meerkats scent mark reliably after emerging from the nest box. Since there is no intervening activity, it appears that the scent mark is deposited directly on the nest box opening. Standing motionless with the head in a tube occurs reliably after running, and immediately before ascending or descending the ledge via the tubes. Standing with the head in the tubes which lead to the window ledges or the nestbox may indicate some ambivalence about entering the tube. Drinking is rarely followed by eating, probably because the food and water bowls were generally geographically separate, and walking is rarely followed by eating or self grooming.

The transitions between the solitary activities of the two focal animals were then analyzed using chi square techniques with all interactive behavior grouped into a single category. This gives a view of the relationship between the solitary acts and the social ones. The resulting matrix had 15 rows and 15 columns. The entries on the major diagonal were all zero since activities were defined in such a way that an act could not follow itself. There were a total of 22922 transitions in this matrix, however, 93/225 cells in the expected frequencies matrix were less than 5. Thus the same caution is advised as for the previous analysis. The observed transition matrix was significantly different from a random distribution, χ^2 (181, _N_ = 22922) = 16931, _p_ < .0001. There were many significant single cells in the matrix and the positive ones are shown in Figure 4. The transitions between these solitary activities and the complex of social activities is of particular interest here. A solitary animal lying down alone appears to "invite" social interactions and in this analysis this activity has no other significant positive transitions. Social interactions also occur while up on the ledge and immediately after coming down from the ledge. Scratching and digging, drinking, and self grooming also often result in social interactions possibly through an allelomimetic mechanism.

In order to confirm these organizational regularities and to look for the transition relationships between the larger classes cf activity that are suggested by the chi square analyses, MDS DEDICOM was applied to the matrix of transitions described above. Since the DEDICOM program will not accommodate a 34 X 34 matrix, no analysis of the full data matrix was possible. The groupings suggested by the chi square analysis of the full data matrix were used to

Figure 4. The significant transitions (p < .001) between the social activities (classified together and shown as an angled box) and all solitary activities (round-cornered boxes). These are the results of a chi square analysis. As in the preceeding two figures, negative transitions are included only where they do not obscure the figure (see the text). Note especially the lines of transition to and from the social activities.


CARRY
EAT
SCRATCH/DIG
WALK
IMMOBILE
RUN
NESTBOX
SCENT MARK
DRINK
SELF GROOM
LEDGE DOWN
HEAD IN TUBES
SOCIAL ACTIVITIES
LIE DOWN
LEDGE UP
POSITIVE
NEGATIVE

group activities into event classes and hence reduce the size of the data matrix to make it acceptable by the program. For example, in the analysis of the social activities, all solitary activities are treated as if they were a single event. In the MDS DEDICOM analyses reported here, the coefficient of determination was plotted to determine the appropriate number of dimensions, and the diagonal entries in the matrix were estimated from the full data matrix. In addition, all analyses were completed using the data in their original units. The advantage of this is that the matrix of relationships between factors can be interpreted in the same units as the original measurements.

The fit-dimensionality curve is shown in Figure 5. The correlations shown here suggest four dimensions and the clusters and transitions are shown schematically in Figure 6. The activities associated with with each factor are shown within the boxes and the transition relationships are indicated by the directional lines joining them. Factor loadings and the matrix of transition frequencies are included in Appendix D. Self grooming, defecation and urination, and locomotion formed a complex labeled self-maintenance. The cluster of activities shown in the upper right of Figure 6 was called foraging and included scratching/digging, eating and carrying (always a food item). The complex of activities in the lower left of the

Figure 5. The fit-dimensionality curve derived by a DEDICOM analysis of the solitary activities. This curve represents the square of the correlation between the data matrix and the matrix estimated by the factor solution at each dimensionality. This figure suggests that the four-dimensional solution is likely the most appropriate one for analysis.

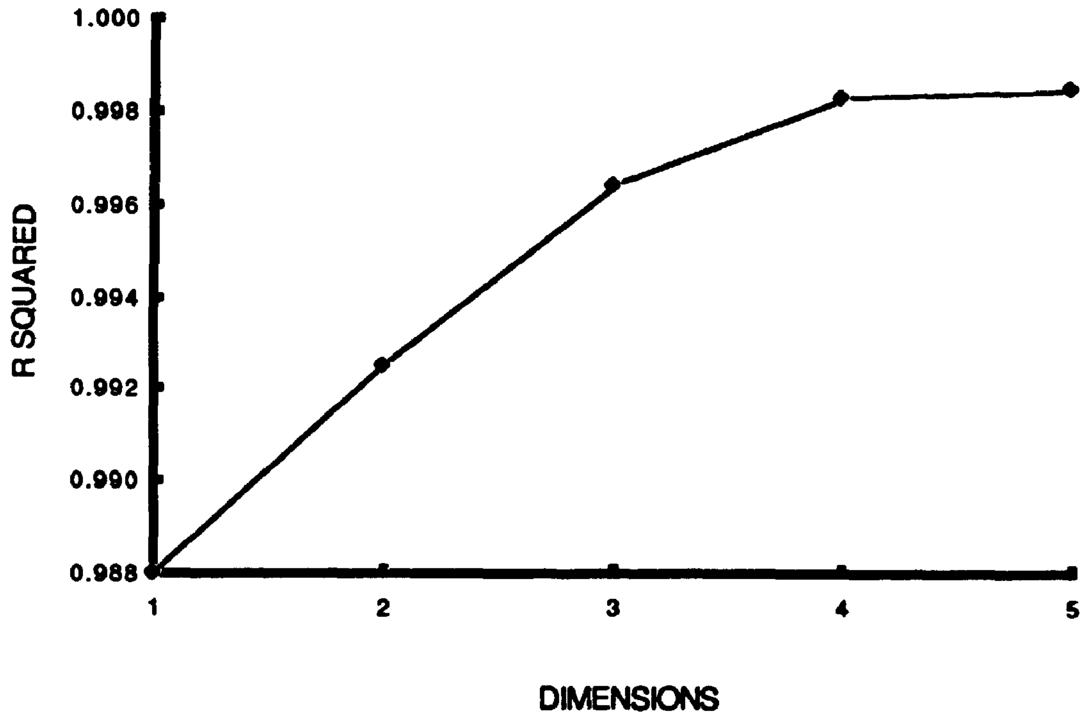

R SQUARED
1.000
0.998
0.996
0.994
0.992
0.990
0.988
1
2
3
4
5
DIMENSIONS

Figure 6. A schematic representation of the factor structure and transition relationships for the solitary activities which resulted from a DEDICOM analysis. The four boxes represent the four dimensions suggested in the previous figure. The activities shown within each box are those which had the highest loading on the particular dimension. Shown as the first entry in each box is an interpretive label. The lines connecting each box represent the relative number of transitions from one dimension to another. The bolder lines represent the largest number of transitions. Note that the asymmetry in the data matrix is represented here as unequal transition frequencies between any two dimensions. For this analysis all interactional activities were classed together as a single social act.

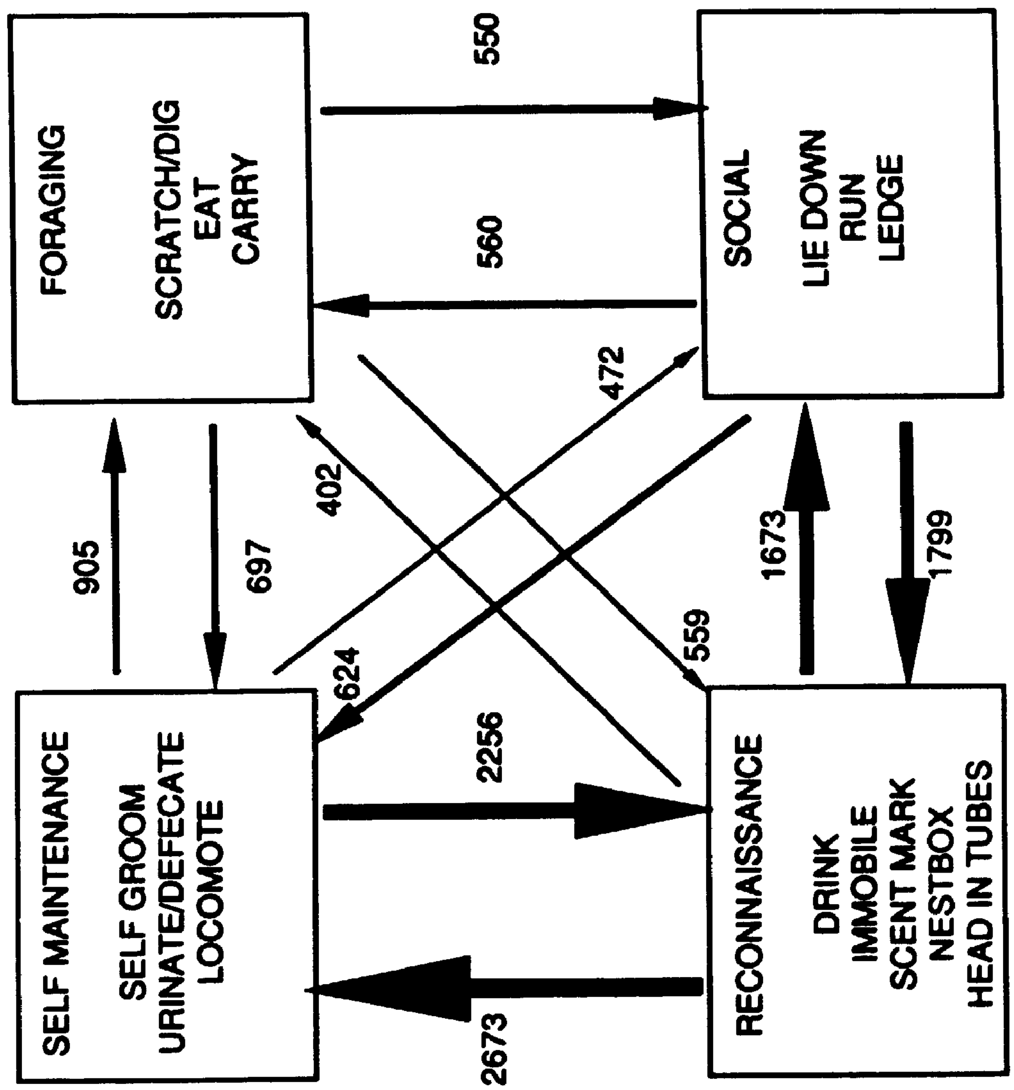

FORAGING
SCRATCH/DIG
EAT
CARRY
SOCIAL
LIE DOWN
RUN
LEDGE
SELF MAINTENANCE
SELF GROOM
URINATE/DEFECATE
LOCOMOTE
RECONNAISSANCE
DRINK
IMMOBILE
SCENT MARK
NESTBOX
HEAD IN TUBES
550
560
472
402
905
697
624
559
1673
1799
2256
2673

figure was labeled reconnaissance since it included alert immobile postures, checking the tubing briefly (head in tubes) as well as scent marking, an activity which included sniffing, scratching at, and rubbing the body on known marking posts. The remaining cluster contained the social activities and hence was labeled the social factor. These dimensions or factors are consistent with those described by the chi square analysis reported above and illustrated in Figure 4.

The transitions from one complex of activities to another, information not available from the chi square analysis, are also shown in Figure 6. The number associated with each line indicates the relative number of transitions between the factors that it joins. There are many transitions among the self-maintenance, reconnaissance, and foraging factors suggesting that these in fact are a separate class of solitary activities. The largest number of transitions to the social factor occurs from the reconnaissance factor with very few from the foraging factor and almost none from the self-maintenance one. This is generally consistent with the flow diagram shown in Figure 2 which is based on a chi square analysis.

<u>Between-Individual Organization</u>.

In order to look more closely at the social behavior components, a new transition matrix showing only frequencies of transition among the social acts was created and analyzed using MDS DEDICOM. For this analysis, all solitary activities were grouped into three categories according to the earlier MDS analysis. The fit-dimensionality curve for these data is shown by the open symbols (All Weeks) in Figure 7. There is a strong suggestion of three factors here and this solution was chosen for interpretation. The factor structure and transition relationships for these three dimensions are shown in Figure 8. Factor loadings and the matrix of transition frequencies are included in Appendix D. All three of the solitary factors as defined in the earlier analysis grouped together to form what is called a Solitary dimension. The social activities grouped themselves into two major classes, described as Active and Passive Interactions. The Passive Interactions are characterized by such activities as resting in contact and allo- and mutual-grooming. The Active Interactions include biting, pushing, clasping, head fencing, pouncing and chasing. This distribution of activities supports that suggested by the chi square analysis presented in Figure 2.

The transitions between these complexes of behavior are also shown in Figure 8. There were relatively few transitions between the Solitary behaviors and the Active Interaction class in either direction. Active Interactions changed into Passive Interactions and vice versa with

Figure 7. Fit-dimensionality curves derived by a DEDICOM analysis of the social activities with the solitary activities grouped into three event classes based on the previous DEDICOM analysis. These curves represent the square of the correlation between the data matrix and the matrix estimated by the factor solution at each dimensionality. The open symbols represent the data for all weeks of the study while the closed ones represent odd and even weeks. There is a suggestion here of four or more dimensions.

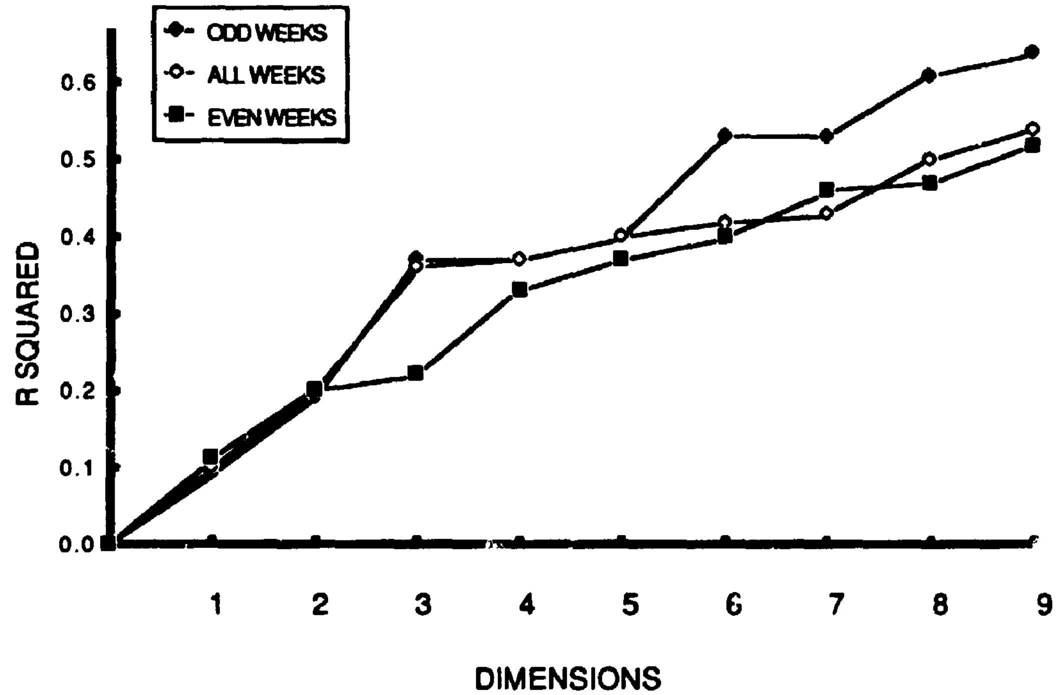
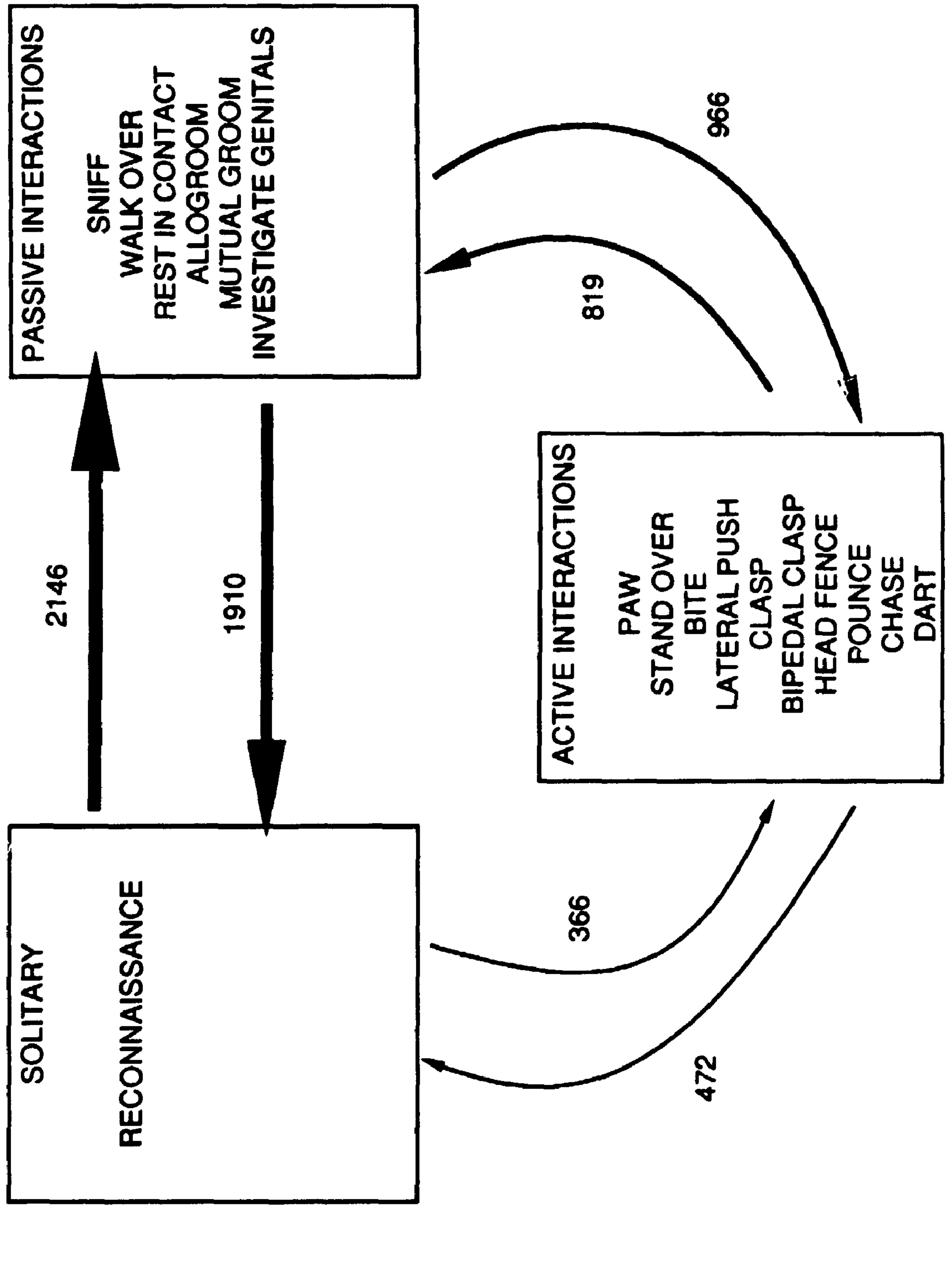

ODD WEEKS
ALL WEEKS
EVEN WEEKS
R SQUARED
0.0
0.1
0.2
0.3
0.4
0.5
0.6
1
2
3
4
5
6
7
8
9
DIMENSIONS

Figure 8. A schematic representation of the factor structure and transition relationships for the social activities. Each box represents one of three dimensions. The activities shown within each box are those which had the highest loading on the particular dimension. Shown as the first entry in each box is an interpretive label. The lines connecting each box represent the relative number of transitions from one dimension to another. The bolder lines represent the largest number of transitions. Note that the asymmetry in the data matrix is represented here as unequal transition frequencies between any two dimensions. For this analysis all solitary activities were classed together according to the output of the DEDICOM analysis of the solitary activities. Note the large number of transitions between the solitary activities and the passive interactions.

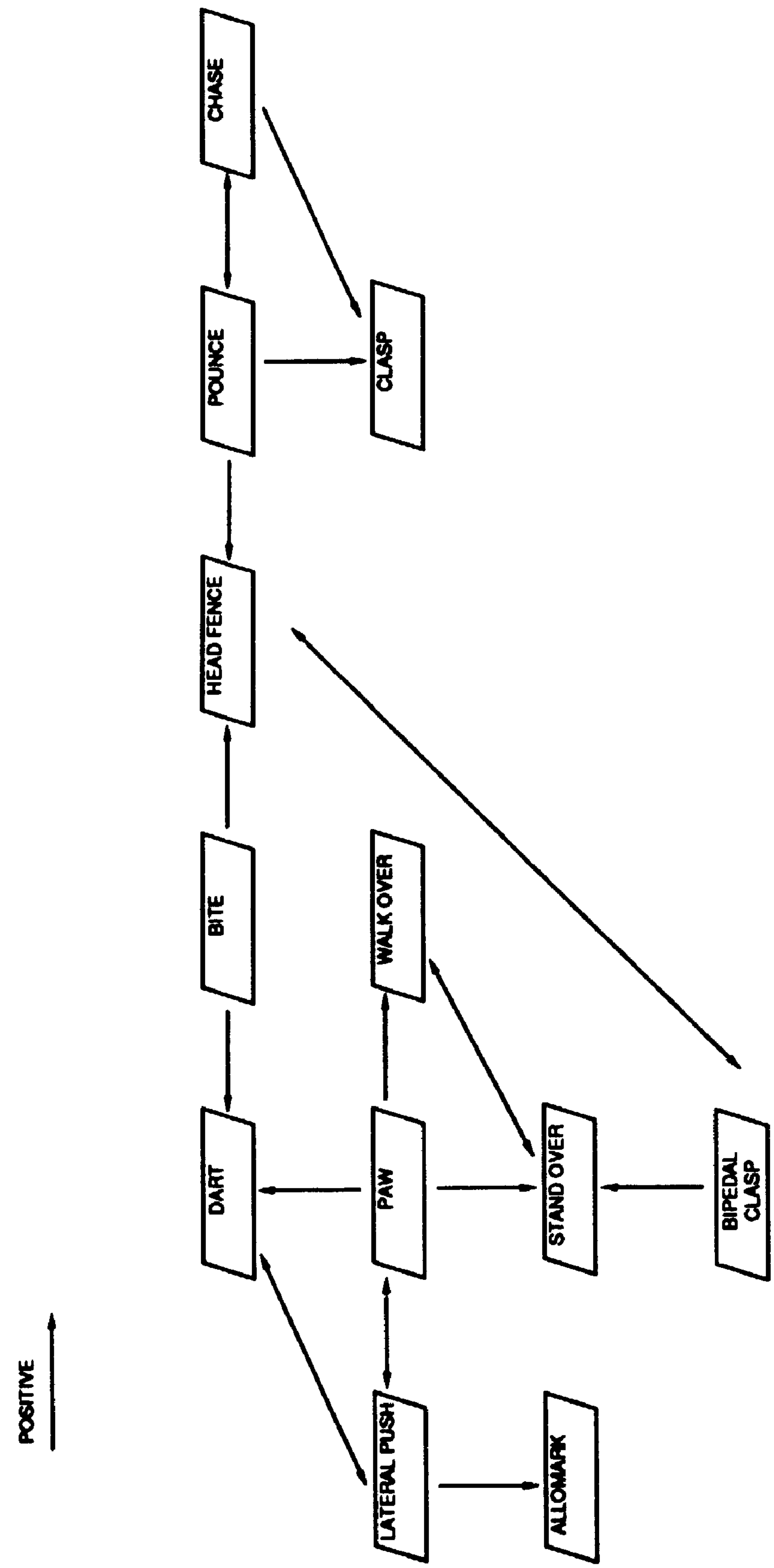

PASSIVE INTERACTIONS
SNIFF
WALK OVER
REST IN CONTACT
ALLOGROOM
MUTUAL GROOM
INVESTIGATE GENITALS
ACTIVE INTERACTIONS
PAW
STAND OVER
BITE
LATERAL PUSH
CLASP
BIPEDAL CLASP
HEAD FENCE
POUNCE
CHASE
DART
SOLITARY
RECONNAISSANCE
2146
1910
966
819
366
472

greater frequency. Interactions appear to begin and end with Passive Interactions since it is here that changes from social to solitary acts occur most frequently.

Similar outcomes were achieved for two subsequent analyses, one for even weeks and one for all odd numbered weeks. These fit-dimensionality curves are included in Figure 7. The factor structure and transition relationships for each of these "split-half" analyses showed the same pattern as that which resulted from the analysis of the full data matrix and illustrated in Figure 8. This suggests a degree of constancy over all weeks in the data set used for all analyses in this study.

<u>Active Interactions.</u> The activities considered part of a group called active interactions are listed in the second group in Table 2. In order to focus specifically on the organization within active interactions, an analysis was completed with a matrix composed only of transitions among the activities classed as active interactions and omitting all transitions to other activity types. This resulted in a 12 X 12 matrix with zeros on the diagonal. The overall chi square is significant suggesting a non-random arrangement of transitions between the elements of active interactions, χ^2 (109, $\underline{N}$ = 4158) = 755.74, $\underline{p} < .001$. Single cell transitions that are significant and positive are schematized in Figure 9. It shows a fairly simple and orderly arrangement

Figure 9. Significant positive transitions (p < .001) between the activities classed as part of the complex called Active Interactions (shown as angled boxes in Figure 2). Transitions to the solitary activities have been omitted. These transition probabilities were obtained using a chi square analysis.

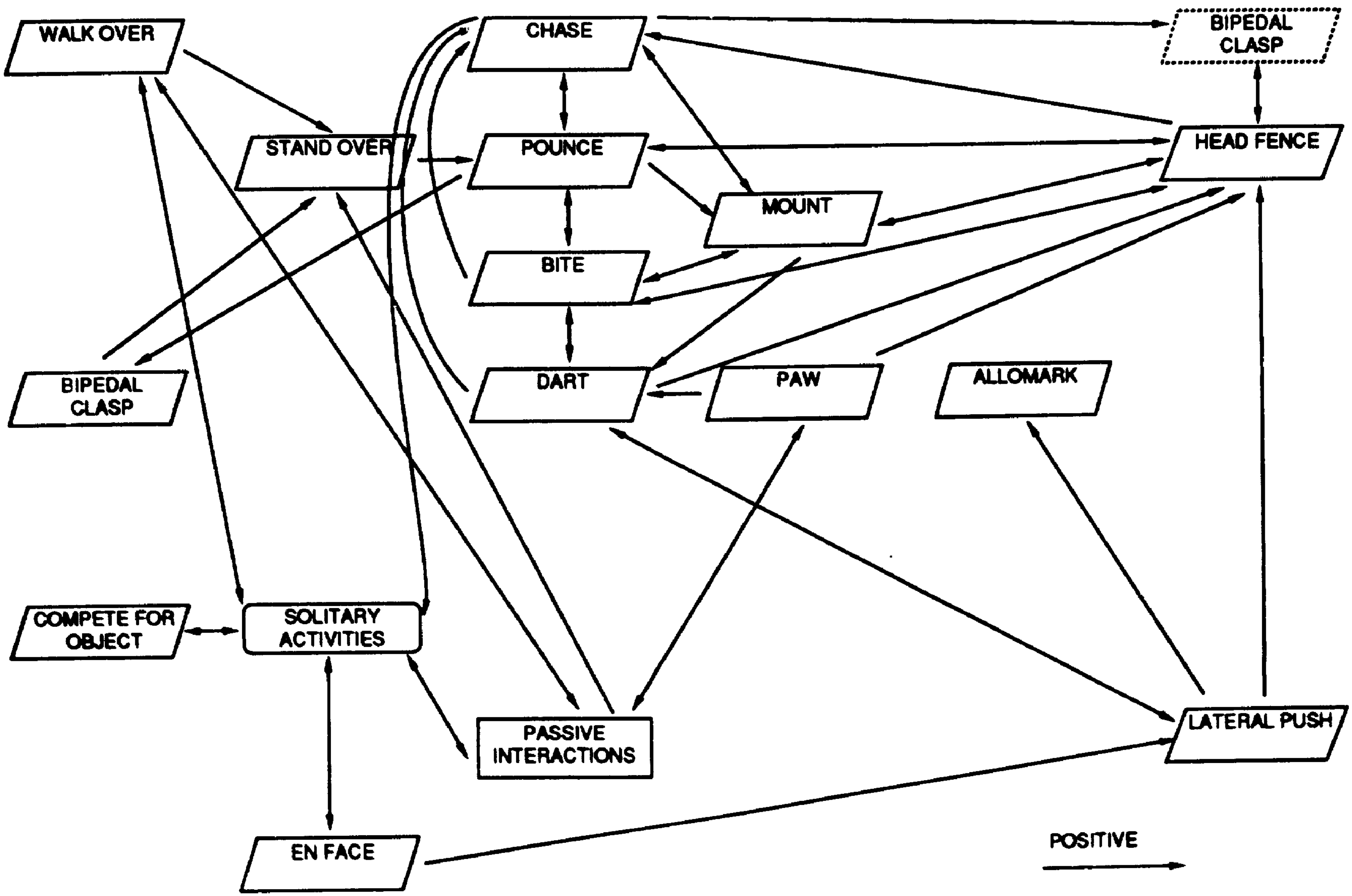

POSITIVE
CHASE
POUNCE
CLASP
HEAD FENCE
BITE
WALK OVER
DART
PAW
STAND OVER
BIPEDAL CLASP
LATERAL PUSH
ALLOMARK

of activities.

A second analysis of the active interactions was completed which included en face and compete for object as part of the active interaction class. In addition, all solitary activites were treated as a single action class and the components of passive interactions were treated the same way. This resulted in a 16 X 16 matrix. As was the case for the solitary activities, the matrix of transition frequencies for active interactions was significantly different from a random distribution, χ^2 (209, N = 15902) = 7713.32, $p < .001$. Of the 256 cells in the matrix, 127 are significant when compared to a conservative critical chi square with 1 degree of freedom; 78 of these are significant at the .001 level. Although it makes for a complex picture, those that are significant and positive are schematized in Figure 10. This offers a somewhat more detailed picture than that shown earlier by Figure 2. Bite, dart, chase, and head fence form little vortices around which many other activities centre. These appear to be "pivotal" activities or "links to" other activities. As reported earlier for the full data matrix, the negative transitions make such a complicated f'ow diagram that they are not included here.

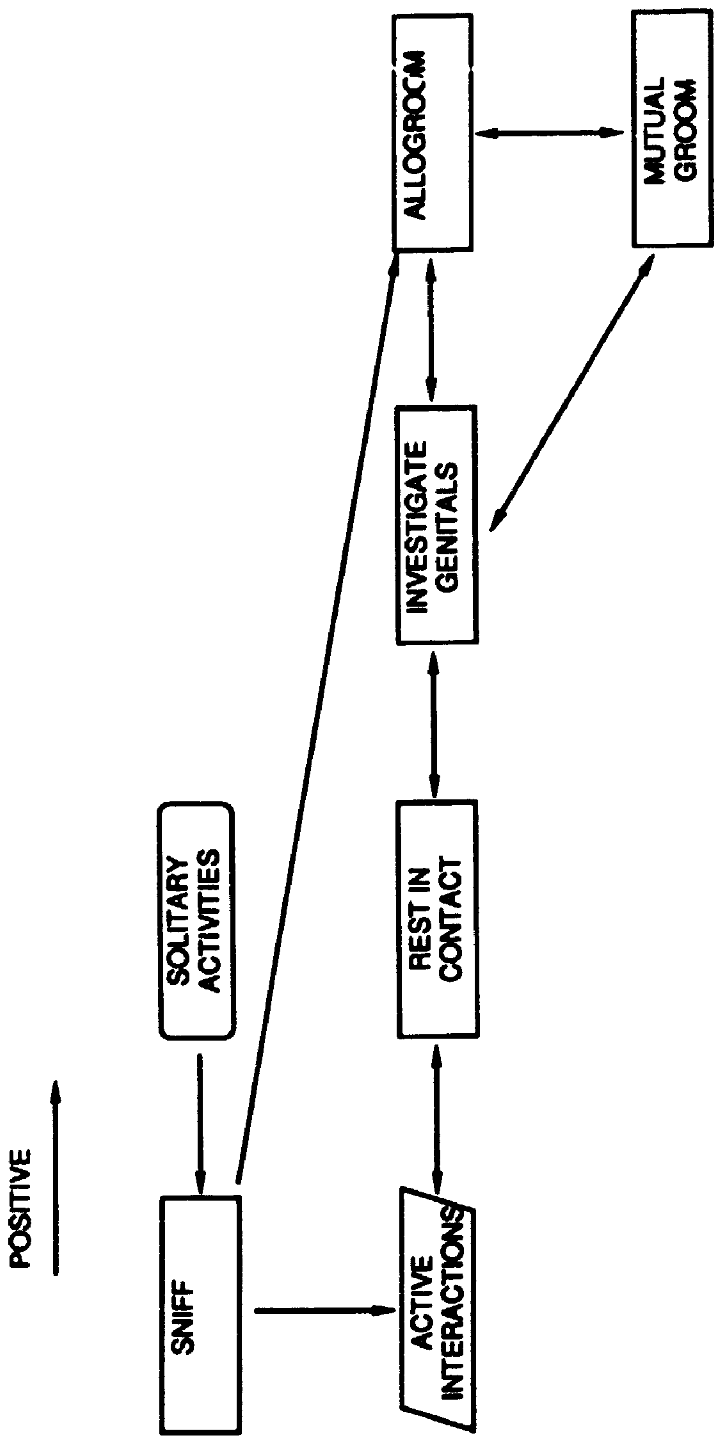
Passive Interactions. Five activities are included in

Figure 10. Positive transitions ($p < .001$) between the active interactions (angled boxes), passive interactions (shown as a single box with square corners) and solitary activities (shown as a single box with rounded corners) derived using a chi square analysis. Note that bipedal clasp appears twice on this figure to minimize the overlap of the lines of transition.


WALK OVER
STAND OVER
CHASE
POUNCE
BITE
DART
MOUNT
PAW
ALLOMARK
BIPEDAL CLASP
HEAD FENCE
BIPEDAL CLASP
COMPETE FOR OBJECT
SOLITARY ACTIVITIES
PASSIVE INTERACTIONS
LATERAL PUSH
EN FACE
POSITIVE

the interaction class called passive interactions. These are shown in a group at the bottom of Table 2 and include allogrooming, mutual grooming, investigating the genital area of another animal, resting or sleeping while in contact with one or more other meerkats, and sniffing at another animal. An analysis was first completed including these specific acts and grouping together all other acts into two classes: active interactions, and solitary activities. The result was an 8 X 8 matrix of transition frequencies. This matrix included 12177 transitions and the overall pattern of organization differed significantly from that predicted by a model of quasi-independence, χ^2 (41, N = 12177) = 5081.65, $p < .001$. This suggests that the activities of the reactor were in some way dependent on the activities of the actor. The cells in the matrix which were significant when evaluated against a chi square with 1 df are plotted in Figure 11. Social sniffing appears to form the link between solitary activities, and the active and passive interactions. Sniffing the pelage of another meerkat and then grooming it can result in reciprocated grooming. Thus sniffing forms a direct pathway into passive interactions also. Allogrooming, mutual grooming and genital investigation form a cluster of activities shown in the lower right of this figure.

Figure 11. A pictorial representation of the positive transitions ($\underline{p} < .001$) between the activities classed as Passive Interactions (shown as boxes with square corners) and all other classes of activity (active interactions in a single angled box and solitary activities in a single box with rounded corneers) as determined by a chi square analysis.


POSITIVE
SNIFF
SOLITARY ACTIVITIES
ACTIVE INTERACTIONS
REST IN CONTACT
INVESTIGATE GENITALS
ALLOGROOM
MUTUAL GROOM

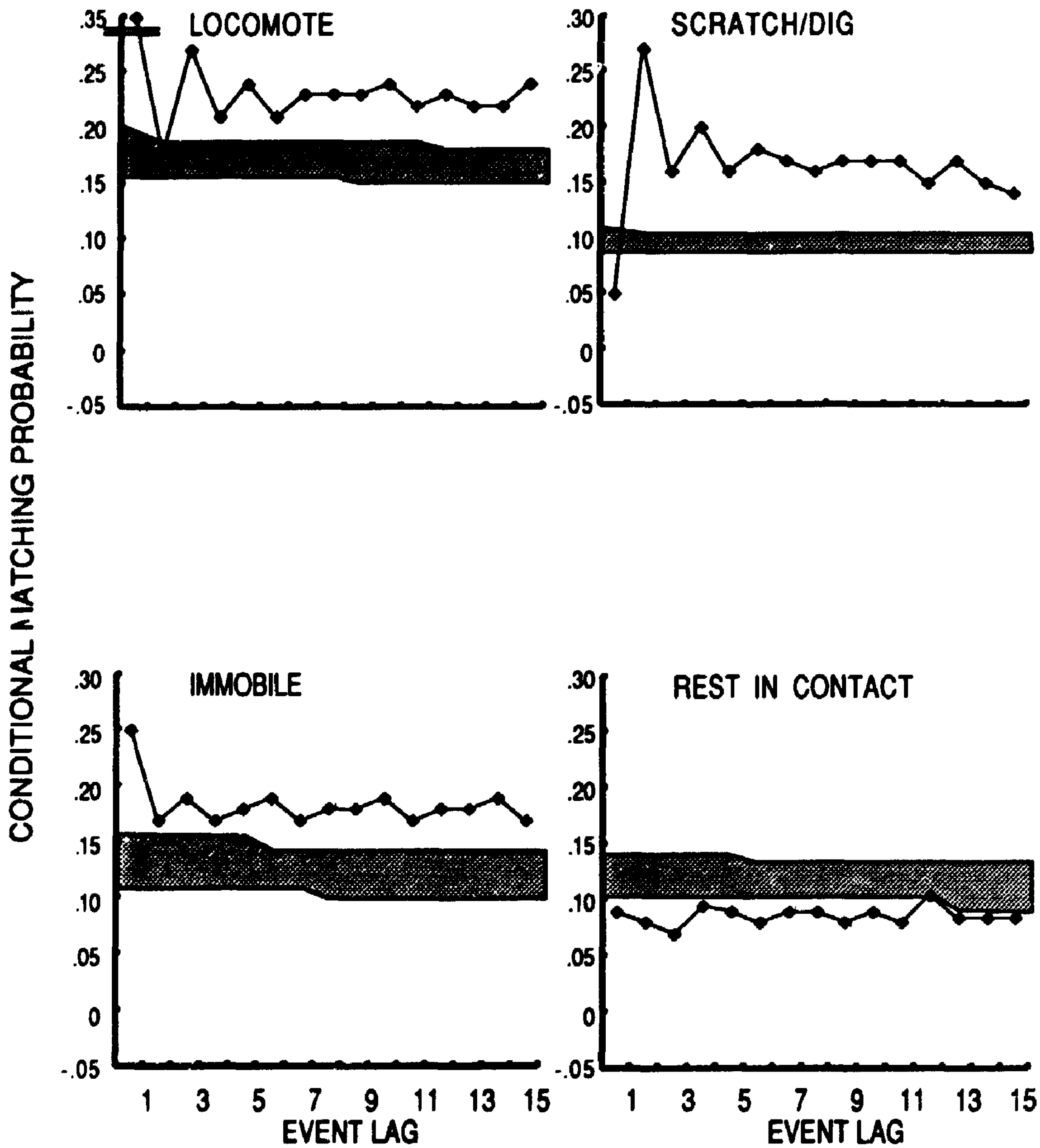
Lag Dependencies.

The chi square and MDS analyses summarized above provide information only about adjacent behavior elements. To assess the possibility that some behavioral events affect the probability of occurrence of more than just a single subsequent event, a lag sequence analysis was conducted for each pair of behavior elements which were linked together in Figure 2. This event sequence analysis evaluated the likelihood of each pair of behaviors up to 15 events later. There are two classes of lag sequence analyses included here -- those for activities within an individual and those for activities between individuals. Illustrative lag profiles are included here as Figures 12 through 17. In these figures the horizontal axis represents the number of subsequent events and the shaded area represents the 99% confidence limits. Probabilities which are above these confidence limits show greater than chance expectancies and suggest that the target behavior somehow facilitates the following behavior through one or more subsequent events. Probabilities which are below these confidence limits suggest that the target behavior suppresses the following behavior for one or more subsequent events. The horizontal axis is shown as a negative number for clarity in these small graphs. The target or criterion activity is shown in bold letters at the bottom of each figure. The matching activity is shown within the body of each individual graph. Several activity pairs showed a transition relationship like that for scratch/dig-locomotion in the upper left-hand panel of Figure 12. In this case, there is an early and a late facilitation of the following activity with a decline to a non-significant probability of occurrence in between. Immobility-run, bipedal clasp-head fence, paw-rest in contact, locomotion-scratch/dig, scratch/dig-eat, and immobile-locomotion show variations of this pattern.

Many other transition profiles looked like that for scratch dig-immobile in the bottom left of Figure 12. In this example, an immobile posture is highly probable following scratch/dig throughout the entire 15 subsequent events. This is also true of the following pairs of activities: pounce-bite, pounce-head fence, pounce-chase, head fence-chase, dart-bite, self groom-allogroom, mutual groom-allogroom, rest in contact-end interaction, bite-head fence, bite-dart, head fence-bite, head fence-pounce, eat-carry, chase-pounce, chase-clasp from above (mount), and locomotion-immobile.

Other temporal relationships are also possible. An activity may inhibit certain other activities following its occurrence. Since the solitary acts of an animal do not follow each other directly, the significant inhibition of

Figure 12. Lag profiles for scratch/dig followed by locomotion, immobile, scratch/dig, and rest in contact. The lags represent the probability of the follow behavior occurring after scratch/dig as the first through fifteenth subsequent activity. The horizontal axis represents the number of subsequent events and the shaded area represents the 99% confidence limits. Probabilities which are above these confidence limits show greater than chance expectancies and suggest that the target behavior somehow facilitates the following behavior through one or more subsequent events. Probabilities which are below these confidence limits suggest that the target behavior suppresses the following behavior for one or more subsequent events. The horizontal axis is shown as a negative number for clarity in these small graphs. The target or criterion activity is shown in bold letters at the bottom of the figure. The matching activity is shown within the body of each individual graph.

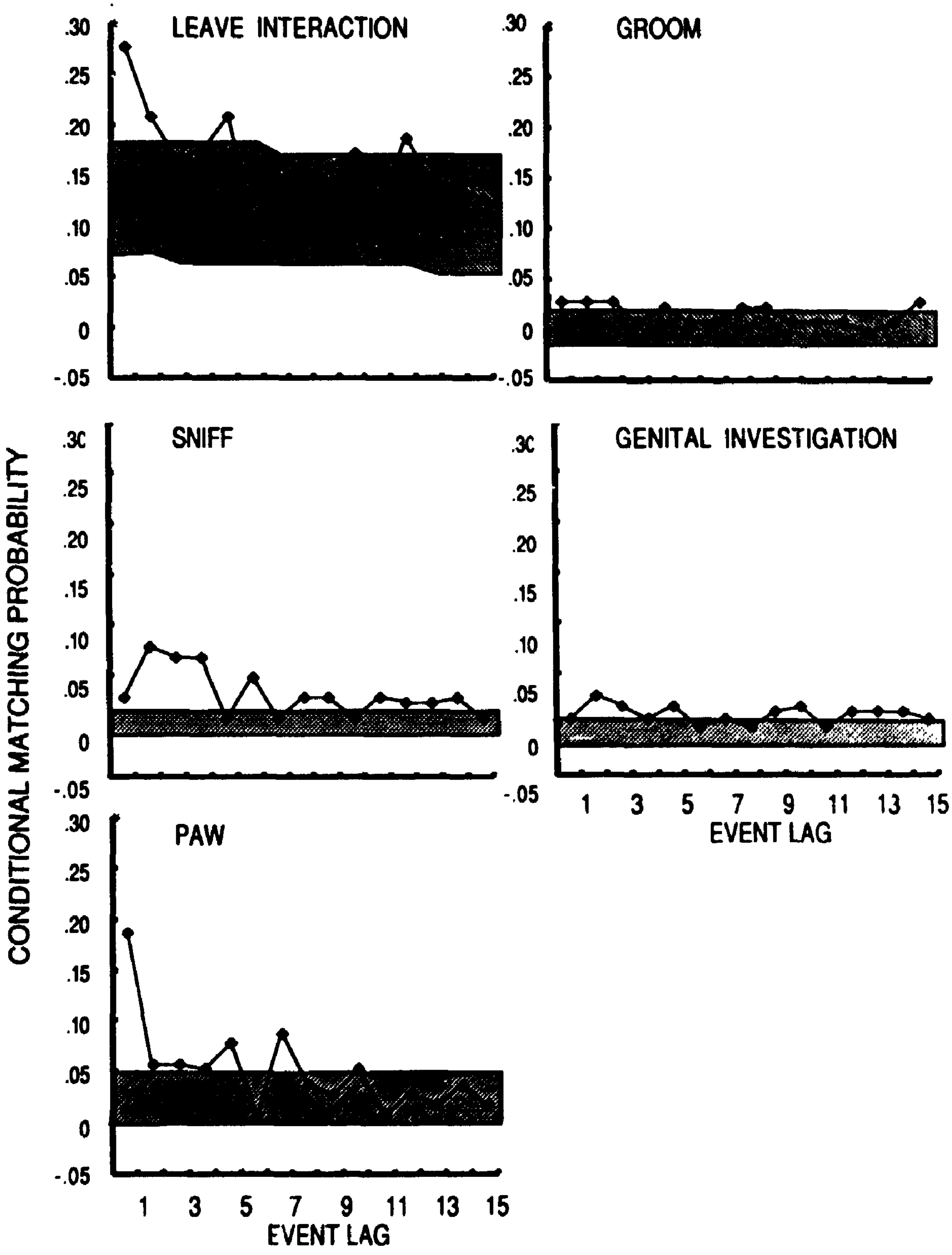

LOCOMOTE
SCRATCH/DIG
IMMOBILE
REST IN CONTACT
CONDITIONAL MATCHING PROBABILITY
.35
.30
.25
.20
.15
.10
.05
0
-.05
1 3 5 7 9 11 13 15
EVENT LAG

SCRATCH/DIG

scratch/dig followed by scratch/dig is an artifact of the coding system used for solitary activities and should be disregarded here. However, the duration of this inhibitory effect may vary, either beginning early or late as is the case for scratch/dig-rest in contact shown in the lower right-hand panel of Figure 12. In each case the "follow" activity is highly unlikely to occur for one or more activities after the occurrence of the criterion behavior. In a few cases the follow behavior was facilitated for only a few subsequent events. This is true for example of sniff-paw, shown in the upper right of Figure 13. This is also true of locomote-drink, immobile-run, immobile-self groom, and leave interaction-run.

Solitary activities such as locomotion, sitting or standing immobile, and scratching at objects are suppressed for up to eight events following social activities such as allogrooming. Social activities such as mutual grooming, sniffing, and pawing are highly likely following allogrooming or resting in contact. Mutual grooming appears to cycle repetitively with passively resting in contact. Sitting or standing immobile is followed only by other solitary activities for as many as 15 subsequent events. Resting in contact, perhaps the most predominant social activity, is inhibited throughout this period. Similar relationships exist between all other "social" and

Figure 13. Lag profiles for sniff followed by leave an interaction, sniff, paw, groom, and genital investigation. The lags represent the probability of the follow behavior occurring after sniff as the first through fifteenth subsequent activity. The horizontal axis represents the number of subsequent events and the shaded area represents the 99% confidence limits. Probabilities which are above these confidence limits show greater than chance expectancies and suggest that the target behavior somehow facilitates the following behavior through one or more subsequent events. Probabilities which are below these confidence limits suggest that the target behavior suppresses the following behavior for one or more subsequent events. The horizontal axis is shown as a negative number for clarity in these small graphs. The target or criterion activity is shown in bold letters at the bottom of the figure. The matching activity is shown within the body of each individual graph.


LEAVE INTERACTION
GROOM
SNIFF
GENITAL INVESTIGATION
PAW
CONDITIONAL MATCHING PROBABILITY
.30
.25
.20
.15
.10
.05
0
-.05
1 3 5 7 9 11 13 15
EVENT LAG

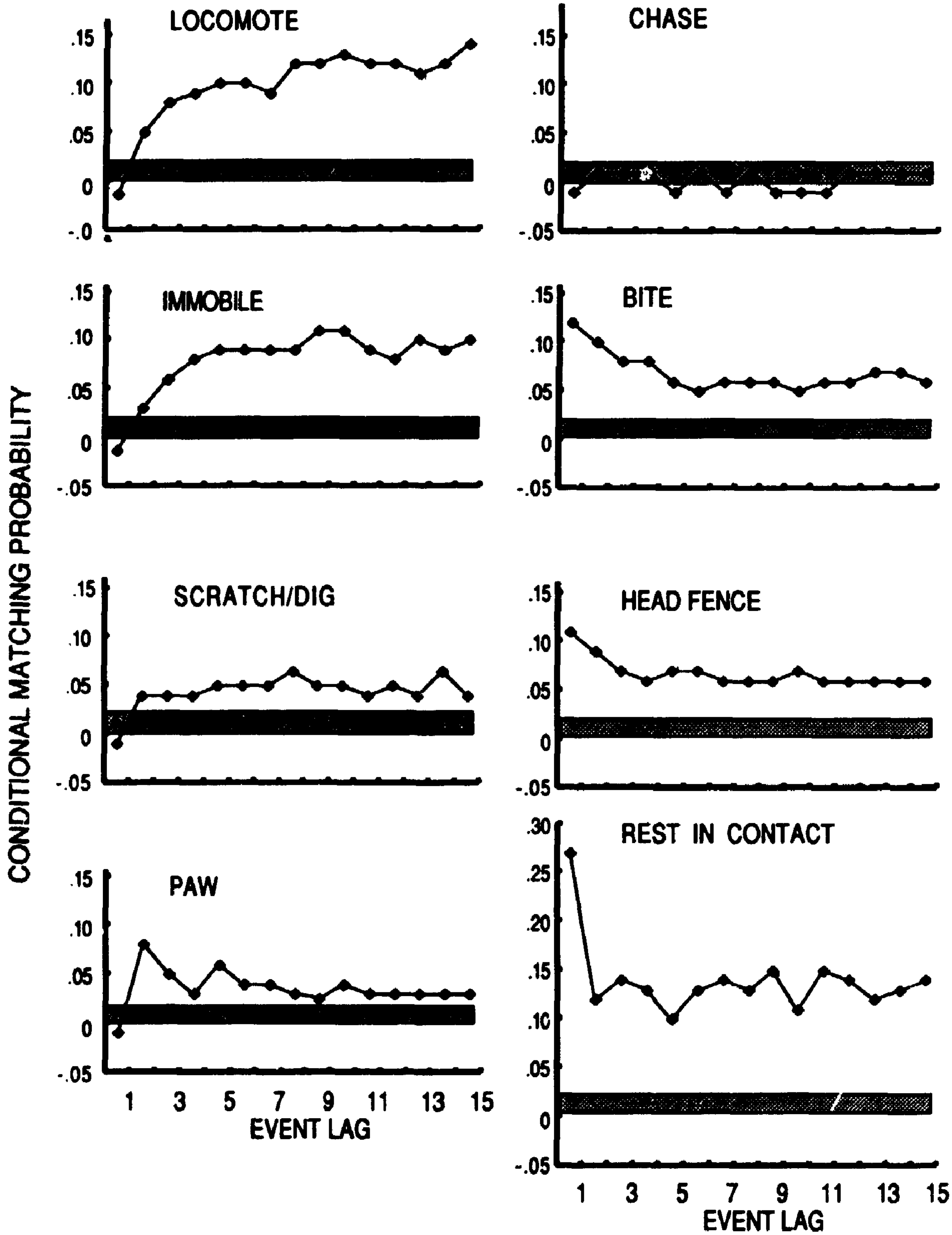
SNIFF

"solitary" activities.

Details of an analysis of the lag dependencies between many of the activities which are classed as part of active interactions are shown in Figures 14 to 17. Figure 14 shows the lag dependencies between PAW and several other activities. These lag dependencies represent the highest conditional transition probabilities. Figure 14 shows that locomote is improbable as the first event following paw but gradually increases to $p = .13$ as the 15th subsequent event. In contrast, rest in contact has a very high probability of following (matching) paw at Lag 1 and this probability decreases over subsequent events.

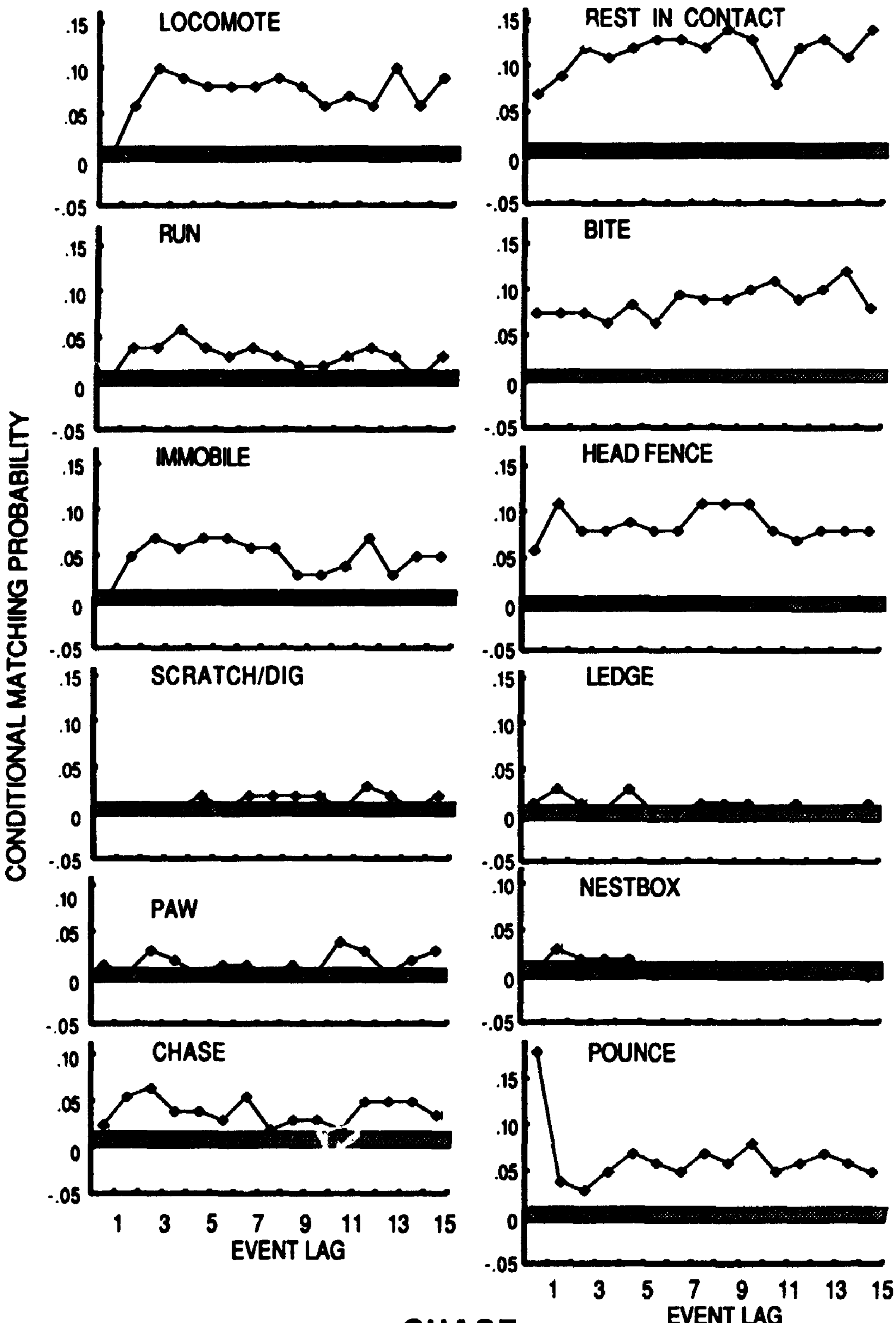
Several activities showed interesting deviations from this pattern. The conditional probabilities and 99% Confidence intervals for event lag matches with CHASE as the criterion behavior are shown in Figure 15. In this case, resting in contact starts out with a relatively low matching probability which gradually increases. The same is true for biting and head fencing following a chase. This is opposite to the pattern shown for paw when matched with these same activities. There are two matching behaviors added to this figure which do not appear in the previous one. Following a chase, animals are likely to enter the nestbox or to ascend to the ledge through the tubes or via the ramps. These two activities do not show significant matching probabilities

Figure 14. Lag profiles for paw showing the conditional probabilities and 99% Confidence Intervals for event lag matches out to a maximum of 15 event lags. The horizontal axis represents the number of subsequent events and the shaded area represents the 99% confidence limits. Probabilities which are above these confidence limits show greater than chance expectancies and suggest that the target behavior somehow facilitates the following behavior through one or more subsequent events. Probabilities which are below these confidence limits suggest that the target behavior suppresses the following behavior for one or more subsequent events. The horizontal axis is shown as a negative number for clarity in these small graphs. The target or criterion activity is shown in bold letters at the bottom of the figure. The matching activity is shown within the body of each individual graph.


LOCOMOTE
CHASE
IMMOBILE
BITE
SCRATCH/DIG
HEAD FENCE
PAW
REST IN CONTACT
CONDITIONAL MATCHING PROBABILITY
.15
.10
.05
0
-.05
.30
.25
.20
1 3 5 7 9 11 13 15
EVENT LAG

PAW

Figure 15. Lag profiles for chase showing the conditional probabilities and 99% Confidence Intervals for event lag matches out to a maximum of 15 event lags. The horizontal axis represents the number of subsequent events and the shaded area represents the 99% confidence limits. Probabilities which are above these confidence limits show greater than chance expectancies and suggest that the target behavior somehow facilitates the following behavior through one or more subsequent events. Probabilities which are below these confidence limits suggest that the target behavior suppresses the following behavior for one or more subsequent events. The horizontal axis is shown as a negative number for clarity in these small graphs. The target or criterion activity is shown in bold letters at the bottom of the figure. The matching activity is shown within the body of each individual graph.


CONDITIONAL MATCHING PROBABILITY
LOCOMOTE
REST IN CONTACT
RUN
BITE
IMMOBILE
HEAD FENCE
SCRATCH/DIG
LEDGE
PAW
NESTBOX
CHASE
POUNCE
.15
.10
.05
0
-.05
1 3 5 7 9 11 13 15
EVENT LAG

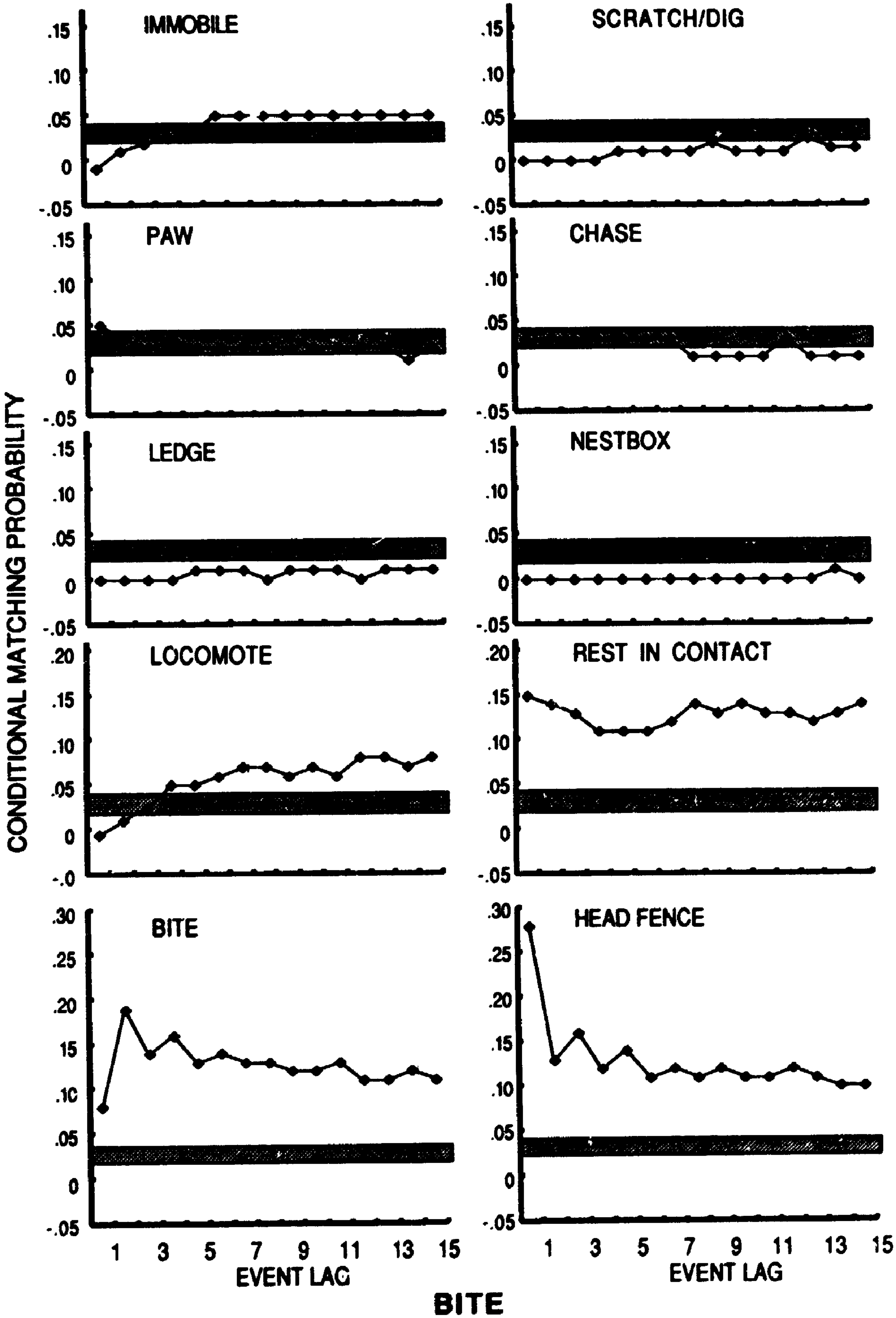
CHASE

with any other social acts.

The lag profiles for BITE as the criterion behavior are shown in Figure 16. Entering the nestbox or ascending to the window ledge have significant negative matching probabilities as mentioned above. The matching relationships for rest in contact and head fence are similar to those shown in Figure 14 with paw as the criterion behavior. Bite, on the other hand shows a profile more like that for chase-bite as shown in Figure 15. Head fencing and biting show a cyclic relationship through to Lag 6. Biting is most probable in Lags 7 and 8. In lag 9, head fencing, biting, and resting in contact are equally probable. At Lag 10 resting in contact once again becomes the most probable behavior. The lag profiles for HEAD FENCE and POUNCE are almost identical to those shown for bite in Figure 16. Head fencing is typically followed by biting and then head fencing is most likely up to Lag 6. At Lag 7 head fencing and resting in contact are equally probable. Finally, in Lags 9 and 10, resting in contact is the most probable activity. Pounce is most likely to be followed by head fencing and resting in contact.

The lag dependencies between BIPEDAL CLASP as the criterion behavior and the other activities which follow it with significant probabilities are shown in Figure 17. These are notable because of the very high probability that

Figure 16. Lag profiles for bite showing the conditional probabilities and 99% Confidence Intervals for event lag matches out to a maximum of 15 event lags. The horizontal axis represents the number of subsequent events and the shaded area represents the 99% confidence limits. Probabilities which are above these confidence limits show greater than chance expectancies and suggest that the target behavior somehow facilitates the following behavior through one or more subsequent events. Probabilities which are below these confidence limits suggest that the target behavior suppresses the following behavior for one or more subsequent events. The horizontal axis is shown as a negative number for clarity in these small graphs. The target or criterion activity is shown in bold letters at the bottom of the figure. The matching activity is shown within the body of each individual graph.


IMMOBILE
SCRATCH/DIG
PAW
CHASE
LEDGE
NESTBOX
LOCOMOTE
REST IN CONTACT
BITE
HEAD FENCE
CONDITIONAL MATCHING PROBABILITY
EVENT LAG
EVENT LAG
BITE

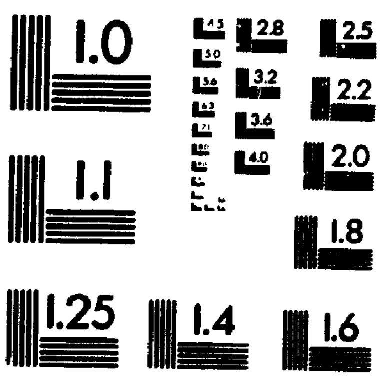
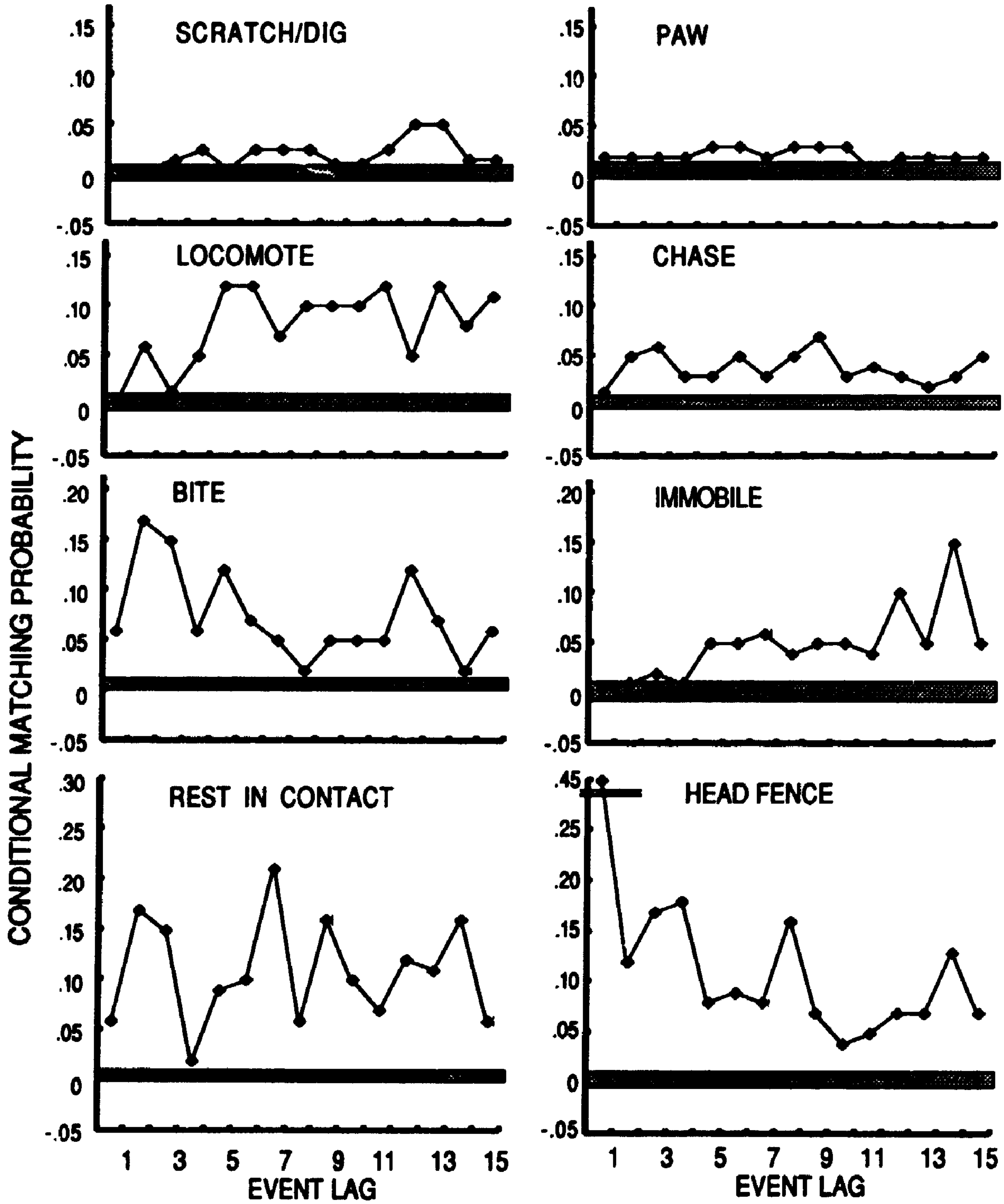

1.0
2.8
2.5
3.2
2.2
3.6
4.0
2.0
1.1
1.8
1.25
1.4
1.6

Figure 17. Lag profiles for bipedal clasp showing the conditional probabilities and 99% Confidence Intervals for event lag matches out to a maximum of 15 event lags. The horizontal axis represents the number of subsequent events and the shaded area represents the 99% confidence limits. Probabilities which are above these confidence limits show greater than chance expectancies and suggest that the target behavior somehow facilitates the following behavior through one or more subsequent events. Probabilities which are below these confidence limits suggest that the target behavior suppresses the following behavior for one or more subsequent events. The horizontal axis is shown as a negative number for clarity in these small graphs. The target or criterion activity is shown in bold letters at the bottom of the figure. The matching activity is shown within the body of each individual graph.



BIPEDAL CLASP

head fencing will follow bipedal clasp (p = .46). Head fencing is the most probable activity at Lag 1. At Lag 2 rest in contact and bite are equally probable followed by head fencing in the next two lag positions. Taken together, these lag frequencies provide an extended version of the relationships presented earlier in Figure 8.

The lag probabilities described can be used to determine chains of behavior that are likely to occur. Some of the highest probabilities are summarized in Table 3. Where more than one behavior was highly probable at any one lag, each is shown. For example, following paw, rest in contact is the most probable event for the first four lags. At lag 5 rest in contact is tied with locomote (suggesting the end of the interaction) for the most probable activity. Rest in contact again becomes the most probable event up to Lag 10 where locomote becomes the following activity with the highest probability. The conditional matching probabilities for several other pairs of activities are almost identical to those shown for paw in Figure 14. These include lateral pushing, "mount", and "dart". The chain of event probabilities, up to Lag 10, for each of these acts is included in Table 3.

Figure 18 shows a schematic representation of these event probabilities. There is evidence of only a single chain of acts which includes chase, pounce and head fence.

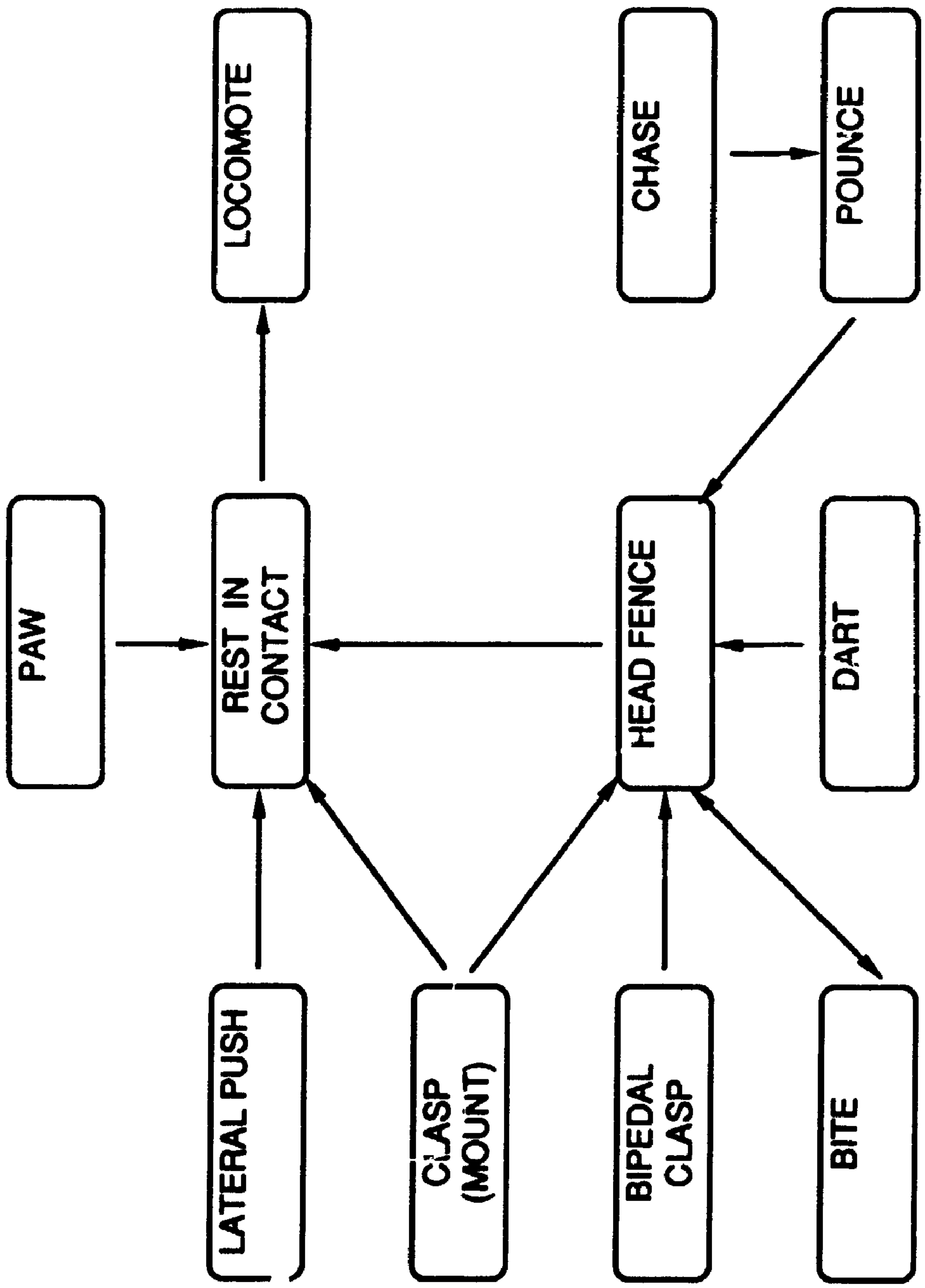
Table 3. The most probable matching behaviour, at lags 1 through 10, for nine social activities as the criterion behaviour.

	LAG									
CRIT	1	2	3	4	5	6	7	8	9	10
PAW	RIC	RIC	RIC	RIC	RIC LOC	RIC	RIC	RIC	RIC	LOC
LPUSH	RIC	RIC	RIC LOC	RIC	RIC	LOC	RIC LOC	RIC	RIC	RIC
MOUNT	RIC HFNC	RIC	RIC	RIC	RIC	RIC	RIC LOC	RIC	RIC	RIC
CHASE	POUN	HFNC	RIC	RIC	RIC	RIC	RIC	RIC HFNC	RIC	RIC
DART	RIC HFNC	RIC	BITE	RIC HFNC	RIC	RIC	RIC	RIC	RIC	RIC
BITE	HFNC	BITE	HFNC	BITE	HFNC	BITE	BITE	BITE	HFNC BITE RIC	RIC
HFNC	BITE	HFNC	HFNC	HFNC	HFNC	HFNC	HFNC RIC	HFNC	RIC	RIC
POUNC	HFNC	RIC	HFNC	RIC	RIC	RIC	RIC	RIC	RIC	RIC
BCLSP	HFNC	RIC BITE	HFNC	HFNC	BITE POUN LOC	POUN	RIC	HFNC	RIC	RIC LOC

KEY:

CRIT Criterion Behaviour
RIC Rest in Contact
LOC Locomote
LPUSH Lateral Push
HFNC Head Fence
POUN Pounce

Figure 18. A schematic representation of the chains of activities suggested by the probabilities summarized in Table 3.


PAW
REST IN CONTACT
LOCOMOTE
CHASE
POUNCE
HEAD FENCE
DART
LATERAL PUSH
CLASP (MOUNT)
BIPEDAL CLASP
BITE

The other activities cluster around resting in contact and head fencing as was the case in all earlier analyses.

Chapter IV

DISCUSSION

The goal of this study was to illustrate multidimensional quantitative techniques in an investigation of patterns of activity in meerkats. Of the three techniques applied, lag sequence analysis was the most difficult to apply and interpret, largely as a function of the number of analyses that had to be completed, interpreted and synthesized. Chi square techniques produced informative results but required a degree of subjective organization on the part of the investigator. MDS DEDICOM provided clear information about the grouping of activities into related classes as well as information about the relationships between these classes. Although there remain some limitations to the application of MDS DEDICOM, it is highly recommended for the analysis of behavioral structure. The results of the application of these techniques to the analysis of the structure of meerkat behavior which has been presented is also subject to some cautionary statements. Although the current study involved a relatively large number of observations of activities, it was focused on two animals in a small family group. Further studies will be required to determine the true representativeness of the findings presented here. Nevertheless, the structural analysis of both solitary and social activities showed a number of regularities about the organization of meerkat behavior. Some of these relationships were shown to last over as many as 15 subsequent events. Taken together, these findings offer a clear picture of how meerkat behavior is organized and illustrate that non-symmetric multidimensional scaling techniques are an extremely useful tool for the investigation of behavioral structure.

Structural Issues

The patterns of transition in interactional and solitary behavior in meerkats are readily apparent. Meerkats reliably engage in three classes of activities. Solitary behavior consists of self maintenance activities such as eating and drinking and self grooming. Passive interactions are characterized by low levels of activity, and lengthy contact with another animal or animals. Active interactions, on the other hand, are fast paced and give the sense of having the potential for agonism.

Solitary acts have already been given an implicit interpretation by the labeling process. The three classes of solitary behavior were labeled foraging, self maintenance and reconnaissance. These are the elemental aspects of living -- feeding, grooming, and maintaining space and security. The passive interactions are low-energy and often lengthy. They may be a critical element in maintaining the social bonds which are essential in any social group. The active interactions are something of an enigma. At first glance they appear to contain elements of agonism yet they are typically not accompanied by vocalizations associated with "annoyance" (Moran, 1980; Sorensen & Moran 1985) and animals were never injured in any way. One is tempted to label them as play. The very rare fights (agonistic interactions which resulted in injury) observed in this captive family, contained only some of these elements. (None of these fights occurred during filming for this study and hence the details are not included.) This argues against an interpretation of developing defense skills. It may be that the active interactions also function to promote social cohesion.

The clusters of activities identified by the analytical techniques applied here are typically interpreted in motivational, functional or evolutionary terms. The results of these analyses suggest two very broad classes of motivational system for meerkats: one characterized by solitary activities and one characterized by interactional behavior. In addition, the interactional classes appear to have two broad sub-classes: one low key and without agonistic overtones and the other containing at least the potential for agonistic motivation. There is an indication that, once initiated, the particular motivational system has a relatively long operational effect. The lag sequence analysis indicated that after a solitary activity such as sitting or standing immobile, other solitary activities are facilitated for as long as 15 events and social behaviors are inhibited through a similar event lag. It remains unclear in the results of this study what the "trigger" is that prompts animals to change from one class of activity to another. In such an interactional system, it is always uncertain whether the observed changes in motivation are due to factors wholly intrinsic to the animals or whether there axists a complex interplay of intrinsic and extrinsic factors. These factors require additional investigation.

When the organization of activity is considered at the broader level of the pattern of transitions between activity classes, a reliable pattern emerges. The solitary activities break down into three subclasses with predictable transitions between them. Only one of these subclasses, called reconnaissance, typically leads to interactional or social behavior. The two major social subcategories, active and passive interactions change back and forth from one to the other with near equal frequency. For example, resting in contact interactions, low energy passive interactions, can be followed by or transformed into high energy potentially agonistic interactions and the reverse occurs equally readily. However, active interactions are much less likely to end with an animal leaving the interaction and engaging in solitary activities than passive interactions are. This suggests that the potentially "more serious" active interactions are degraded into low key ones before the interaction is terminated.

The results of this study present some indicators of what activities typically terminate social interactions but it is not clear from these results how these interactions generally begin. It may be that "start" activities vary a great deal and thus do not have very high probabilities. Hence they would not predominate in the figures included previously. There is, however, some indication that interactions begin and end with passive interactions since it is there that changes from social to solitary acts occur most frequently.

These results also offer some insight into the communication system in existence in this social species. Within any social group, signalling information about individual identity, competitive status, and motivational state are particularly important. The solitary activities show the greatest degree of dependence or the strongest transition patterns, suggesting that the motivational system within a single animal is the most predictable both by the observer and by conspecifics. This dependency decreases for interactional behavior. This is not unexpected since now the motivational systems of at least two animals come into play and hence predictability is diminished. Active interactions show more independence than passive interactions. This suggests that answering the question "What comes next?" is more difficult in active interactions. This makes sense if one considers active interactions to have an agonistic overtone. In a non-agonistic situation, it is appropriate to let your social partner know exactly what it is that you are likely to do next. However, manipulating information through such tactics as bluffing or mimicry may play an important role in communication in potentially agonistic situations (Wiley, 1983).

The lag sequence analysis presented here is of limited value. The number of pairs of activities included in the results is severely restricted. Since every possible 2-act combination from a set of 34 activities represents a tremendous number of lag profiles, only a few representative ones have been included here. Hence the relationships formulated must be considered tentative and incomplete. What they do suggest, however, is that meerkat behavior is not organized in a linear fashion, but rather as clusters of activities (see, for example, Dawkins, 1976). This very finding may be limiting on the appropriateness of this technique since it has typically been applied in order to identify chains of activities. In this case, the organization of meerkat behavior does not seem to fall into this type of arrangement.

It seems that the overall organization of the behavioral system in meerkats has multiple inputs and multiple outputs. That is, a given action may be called into play by different motivational systems. For example, pawing at another meerkat appears in both the active and passive interactions and also is linked to scent marking, considered a solitary activity. There also appear to be multiple converging outputs which result in small clusters of activities which group around another single act. That is, there are multiple routes to certain activities. An organizational pattern such as this has typically been called a lattice hierarchy (Gallistel, 1980; Mook, 1987). In such a system, a given action may be called into play by different motivational systems, higher up in the hierarchy, on different occasions. In other words, the lines of influence cross each other to form a lattice. Such organization provides for a great deal of flexibility of behavior. It makes specific actions into general-purpose tools or modules which can be put to different uses at different times (Mook, 1987). This may explain the relationship between the activities classed here as active interactions and the very few serious agonistic interactions witnessed. Under different circumstances some of the same activities can be called into play with very different consequences.

This description of the organization of behavior as a lattice hierarchy seems to be appropriate for the activities of the meerkats observed. There certainly was no clear evidence of linear chains of activities. However, the clustering of activities may have been tighter than what would be expected from the description of lattice hierarchies described above. At present, however, it appears to be a good working description of the organizational principles at work here.

Methodological Issues

It is unfortunate that a DEDICOM analysis of the full data matrix was not possible. Such an analysis awa.ts program revision. The chi square analysis suggested three groups of activities and it is expected that DEDICOM would have produced a similar result. Where direct comparison was possible, the DEDICOM analyses replicated the chi square analyses with fidelity. The advantage of the DEDICOM approach is twofold. First it provides explicit clustering and, second, it provides additional information about lines of transition between the clusters of acts. These are tremendous advances over traditional chi square approaches.

The DEDICOM program is relatively straightforward to use. Decisions about dimensionality, rotation, and transformations are simple to implement. And, MDS DEDICOM is specifically designed to deal with data which are non-spatial. This simplicity and appropriateness make it the technique of choice in instances where asymmetric matrices are involved. Having a tool that is specifically designed for the type of data matrix to be analyzed is extremely valuable. The added benefit of ease of application makes it more appealing. The advantage of having a non-symmetric technique that gives not only clustering information but also details about how the clusters are related makes the technique highly useful to the student of the organization of behavior.

The lag sequence techniques applied addressed the question of the importance of time as a factor in the organization of behavior. Only a very limited sample of the possible pairs of acts has been reported here. A full analysis of all combinations of activities in a study such as this is mind-numbing to contemplate. As a consequence, the lag sequence analyses included here represent only a small segment of the possible temporal relationships and thus the picture presented is, of necessity, incomplete. A more parsimonious approach is clearly desireable. The development of a three dimensional MDS DEDICOM program will permit a full time- or event-lagged analysis with a much less complex output. Thus answering the question 'Is time an important factor?' will become far simpler. Other issues may be resolved by three dimensional analyses as well. By using time in the sense of chronological age, developmental factors may be discovered. If time is used in the sense of the duration of activities, then interesting differences in the reactions of animals to short duration activities as compared to their reactions to long-duration activities may uncovered. This will permit attempts to answer the question "Is Behavior X different and/or does it have differential effects on a social partner when it has a long rather than a short duration?" If the third dimension was age or sex, then MDS DEDICOM may prove useful in discriminating differences in age or sex classes thus giving the tool the characteristics of discriminant analyses.

There are many advantages of applying multidimensional techniques to data sets such as those created in ethological investigations. The primary ones are simplification, quantification, and explanation. Approaches such as MDS DEDICOM reduce the data matrix to a smaller number of clusters or dimensions using appropriate quantitative techniques. These dimensions are then interpreted using explanatory concepts such as causation. By explaining the clusters, one can offer a causal analysis of the simultaneous effects of several activities.

There are several additional advantages specific to MDS DEDICOM. In the first place it offers less subjective decision criteria for estimating dimensionality than traditionally applied. Fit vs error curves permit investigators to estimate dimensionality without having to invoke an _a priori_ interpretation. This makes factor analysis a discovery process. Second, it permits the estimation of the diagonal cell values by an iterative process that utilizes all off-diagonal entries in the estimation process. This is valuable since random error affects the diagonal elements to a greater degree than it does off-diagonal elements. The third consideration is rotational indeterminacy. In the technique applied in this study, rotational indeterminacy persists. However, this is not true of three dimensional factoring techniques. This makes three dimensional approaches even more appealing. The result is that MDS DEDICOM offers a description of the observed non-spatial relations in terms of latent non-spatial relations of the same type as the surface relations. These relationships among the clusters reproduce the systematic patterns in the observed data matrix. And, they do so with a minimum of quantitative limitations.

Further Research

Meerkat behavior shows all the richness and complexity of a well-choreographed stage play in several acts. The structure of activities within and between individuals is discernable using multidimensional statistical techniques. The activities that meerkats are likely to engage in exhibit quite a reliable pattern in solitary and in "friendly" situations while this plan is less obvious in potentially agonistic ones. In order to uncover developmental factors, these investigations must start earlier, sample more frequently, sample more and larger groups of animals, and, ideally, sample later in the lifespan as well.

Despite the fact that the picture at present is still incomplete and subject to verification, a knowledge engineer attempting to program a meerkat robot would have a very good idea of where to begin. In Aristotelian terms, the matter and the forces have been outlined. The matter consists of the activities described for the species and the forces are shown in the patterns of relationship that link these acts. What remains is to further clarify the observed relationships for this particular species; expand them to other levels of organization within a social group, perhaps using the Hinde (1976) model; and to look for developmental regularities as well. Appropriate tools, applicable to this type of analysis are now available and relatively straightforward to apply. It is expected that, in future, techniques such as MDS DEDICOM will be regularly applied by ethologists as the tool of choice. The advantages are clear and the results can be strikingly simple. This is no small advancement.

APPENDIX A

Shown below are the observed activities recorded for Charles on 30 May 1983 beginning at 3:11 p.m. The first column represents the minutes and seconds of the observation period, the next three columns represent the initiator, action and object of the action. For example, the timer showed 22 seconds at the beginning of this observation session and thus the session will end when it shows 1522. The entries are shown columnwise with two columns per page. Using the descriptions included in the Methods Section, the six entries beginning at 6 minutes and 41 seconds into the observation (0641) are interpreted as follows. Charles (14) stands immobile (16) sniffing some object (09). Two seconds later (0643) he begins scratching (18) at some miscellaneous object (04) and continues for 36 seconds until he is interrupted by Diana (15) at 0719. Diana lies down in passive contact (26) with Charles at this point and they maintain this passive interaction until Diana leaves the interaction (40) at 0721. When the interaction terminates, Charles (14) is scratching (18) at some object (04) (and may have been throughout the interaction). Four seconds later (0725) Charles (14) begins to walk around (14) on the floor (01) of the enclosure.

TIME	WHO	WHAT	OBJECT
0022	14	26	11
0022	14	40	11
0022	14	14	01
0025	14	26	13
0025	14	26	15
0027	14	34	13
0029	13	27	14
0030	13	32	14
0032	13	26	14
0037	10	26	14
0037	13	35	14
0037	13	25	14
0039	10	24	14
0040	10	26	14
0042	15	32	14
0044	13	34	14
0045	13	26	14
0047	10	40	14
0048	14	40	13
0048	14	40	15
0048	14	14	01
0050	14	10	01
0107	14	14	01
0113	14	16	04
0117	14	14	01
0124	14	16	04
0125	14	14	01
0127	14	16	02
0128	14	16	09
0136	14	14	01

TIME	WHO	WHAT	OBJECT
0140	14	16	02
0141	14	14	01
0143	14	18	04
0155	14	14	01
0200	14	10	01
0200	14	26	12
0214	12	31	14
0229	14	40	12
0229	14	10	01
0243	14	14	01
0246	14	26	12
0248	14	40	12
0248	14	14	01
0250	14	16	02
0255	14	14	01
0258	14	10	01
0402	10	26	14
0437	10	40	14
0445	14	14	01
0447	14	18	03
0448	14	14	01
0450	14	10	01
0456	14	14	03
0458	14	13	04
0459	14	14	01
0500	14	16	02
0505	14	14	01
0506	14	10	01
0508	14	14	01
0510	14	16	09

TIME	WHO	WHAT	OBJECT
0513	14	18	04
0515	14	14	01
0517	14	16	09
0518	14	14	01
0520	14	20	02
0536	14	14	01
0537	14	16	04
0538	14	14	01
0540	14	16	04
0541	14	13	05
0546	14	16	02
0547	14	13	01
0552	14	14	01
0558	14	16	04
0603	14	16	09
0607	14	14	01
0611	14	16	01
0612	14	16	02
0616	14	14	01
0618	14	16	09
0620	14	14	01
0625	14	21	05
0627	14	16	04
0630	14	14	01
0631	14	16	04
0632	14	16	02
0638	14	14	01
0641	14	16	09
0643	14	18	04
0719	15	26	14

TIME	WHO	WHAT	OBJECT
0721	15	40	14
0721	14	18	04
0725	14	14	01
0730	14	26	15
0733	15	40	14
0733	14	14	01
0737	14	16	02
0746	14	14	01
0749	14	16	02
0759	14	14	01
0802	14	16	04
0802	14	14	01
0805	14	18	04
0805	14	26	15
0805	14	26	12
0811	15	40	14
0824	12	40	14
0824	14	18	04
0830	14	26	12
0845	10	26	14
0857	15	26	14
0857	13	26	14
1016	13	40	14
1035	13	26	14
1040	15	27	14
1042	15	32	14
1045	15	27	14
1046	15	31	14
1047	15	26	14
1105	14	40	15

TIME	WHO	WHAT	OBJECT
1105	14	40	10
1105	14	40	12
1105	14	40	13
1105	14	14	01
1105	14	16	05
1107	14	10	01
1109	14	14	01
1110	14	16	05
1113	14	14	01
1116	14	21	05
1121	14	14	01
1127	14	21	05
1130	14	18	04
1146	14	16	09
1150	14	16	05
1157	14	21	01
1158	14	21	05
1202	14	14	01
1206	14	16	09
1206	14	18	04
1209	14	14	01
1215	14	18	04
1216	14	14	01
1217	14	18	04
1217	14	26	10
1217	14	26	12
1217	14	26	13
1230	14	40	10
1230	14	40	12
1230	14	40	13

TIME	WHO	WHAT	OBJECT
1230	14	16	04
1232	14	16	02
1236	14	18	04
1236	14	26	12
1236	14	26	10
1236	14	26	13
1259	15	26	14
1307	15	40	14
1326	14	40	10
1326	14	40	12
1326	14	40	13
1326	14	14	01
1336	14	16	09
1344	14	10	01
1345	14	14	01
1347	14	10	01
1351	14	14	01
1353	14	10	01
1437	14	16	05
1439	14	10	01

APPENDIX B

```
C
C
C
C       PROGRAM TO READ A DATA SET OF VARIABLE SIZE
C       AND DO A CHI SQUARE ANALYSIS (CSA) AND
C       AN INFORMATION THEORY ANALYSIS (ITA)
C
C                   PROGRAM WRITTEN BY L. SORENSEN
C                            FEBRUARY 1987
C
C**********GOODMAN OPTION FOR ZEROS ON THE DIAGONAL*********
C
C       PROGRAM WILL PROMPT THE USER TO CHOOSE BETWEEN A
C       NORMAL CHI SQUARE ANALYSIS AND ONE FOR SUCH AN
C       ANALYSIS FOR A MATRIX WITH ZEROS ON THE DIAGONAL.
C       IF THE USER CHOOSES THE ZERO-DIAGONAL OPTION,
C       THE PROGRAM WILL PROMPT FOR THE NUMBER OF ITERATIONS
C       DESIRED.  THE PROGRAM WILL THEN USE THE ITERATIVE
C       METHOD SUGGESTED BY GOODMAN (1968, 1984) TO SET UP
C       THE MATRIX OF EXPECTED VALUES.
C
C**********************************************************
C
C
C       MAXIMUM MATRIX SIZE IS 50 X 50
C
C
C
C       THE USER WILL BE PROMPTED FOR THE INPUT AND OUTPUT
C       FILE NAMES
C
C
C       THE PROGRAM EXPECTS THE INPUT TO BE IN THE FOLLOWING
C       FORMAT:  6X,10I5/   THAT IS, UP TO 10 COLUMNS PER
C       LINE AND CONTINUED ON THE NEXT LINE IF THERE ARE
C       MORE THAN 10 COLUMNS.  EACH ROW OF INPUT MUST BEGIN
C       6 SPACES OVER
C
C
C       THE FIRST ROW OF THE DATA SET MUST CONTAIN THE NUMBER
C       OF ROWS AND COLUMNS USING THE FORMAT 10X,2I5
C
C
C
C       THE PROGRAM CALCULATES CRITICAL CHI SQUARE VALUES IF
C       df > 30
C
```

```
C
C
       COMMON MAT(50,50),LRT(50),LCT(50),LGT,EFL(50,50),
      *ECL(50,50),OPM(50,50),PRT(50),PCT(50),HMAX,H,
      *HR,HC,HRC,HT,HTP,RI,RED,M,N,ITRIP,ITALLY,CHIT,MTALLY,
      *KNT,SD,SRT(50),RPR(50),SCT(50),CPR(50),SIGMA(50,50),
      *A(50),B(50),ITER,NITER,DENOM,P(50,50),TD
       DIMENSION SIGN(50,50)
       CHARACTER AAAA*10,BBBB*10
C
C
C
       WRITE(6,211)
211    FORMAT(5X,'INSERT THE INPUT FILE NAME IN THE FORMAT
      * ATEST1.SET'/)
       READ(5,3)AAAA
3      FORMAT(A10)
       WRITE(6,213)
213    FORMAT(5X,INSERT THE OUTPUT FILE NAME IN THE FORMAT
      * ATEST1.DAT'/)
1345   FORMAT(10X,A10)
       READ(5,3)BBBB
5      FORMAT(A10)
       OPEN(UNIT=25,FILE=AAAA)
       OPEN(UNIT=26,FILE=BBBB)
       WRITE(26,13)AAAA
13     FORMAT(30X,'INPUT MATRIX IS:  ',A10)
       DO 313 I=1,50
               LRT(I)=0
               LCT(I)=0
               PRT(I)=0
               PCT(I)=0
               DO 313 J=1,50
                     MAT(I,J)=0
                     OPM(I,J)=0
                     SIGN(I,J)='     '
                     EFL(I,J)=0
                     ECL(I,J)=0
313    CONTINUE
       LGT=0
       ITRIP=0
C
C
C
       READ(25,11)M,N
11     FORMAT(10X,2I5)
       DO 10, I=1,M
               READ(25,122)(MAT(I,J),J=1,N)
122            FORMAT(6X,10I5/10I5/10I5/4I5)
```

```
10      CONTINUE
C
C
C       **************    NOTE     *****************
C
C       IT WILL BE NECESSARY TO REVISE THIS
C       READ FORMAT IF THE FORMAT OF YOUR DATA
C       FILE DIFFERS FROM THIS OR IF YOUR MATRIX
C       HAS MORE THAN 20 COLUMNS IN IT
C
C       ******************************************
C
C
C       BEGIN CALCULATIONS AND OUTPUT TO .DAT FILE
C
C
820     DO 735 I=1,M
                DO 735 J=1,N
                      LRT(I)=LRT(I)+MAT(I,J)
                      LCT(J)=LCT(J)+MAT(I,J)
                      LGT=LGT+MAT(I,J)
735     CONTINUE
C
C
C
C       CALL SUBROUTINE   NORMAL   OR   SUBROUTINE   NODIAG
C       TO CALCULATE CHI SQ VALUES
C
C
        WRITE(6,703)
703     FORMAT(1H ,'IF YOU WISH ZERO-DIAGONALS SOLUTION
       * INSERT 2')
        WRITE(6,7003)
7003    FORMAT(1H ,'OTHERWISE INSERT 1 WHEN PROMPTED FOR THE
       * TYPE OF ANALYSIS',1H )
C
C
C
        WRITE(6,704)
704     FORMATH0,10X,'INSERT 1 OR 2')
        READ 5,706)NNNN
706     FORMAT(I1)
        IF(NNNN.EQ.1)GOTO 707
C
C
C
        WRITE(26,12)
12      FORMAT(10X,'THE GOODMAN PROCEDURE WAS USED FOR
       * ESTIMATING EXPECTED FREQUENCIES')
```

```
C
C
C
      CALL NODIAG
      GOTO 708
C
C
C
707   CALL NORMAL
C
C
C     PRINT TRANSITION MATRIX AS READ
C
C
708   X="TMAT"
      WRITE(26,230)X
883   ITRIP=ITRIP+1
      CALL IXOUT(MM,NN)
      WRITE(26,46)(I,I=NN,MM)
      DO 210 I=1,M
            WRITE(26,133)(I,(MAT(I,J),J=NN,MM),LRT(I)
133         FORMAT(7X,I5,50I10)
210   CONTINUE
      WRITE(26,242)(LCT(J),J=NN,MM),LGT
      IF(M.GT.(ITRIP*10))GOTO 883
C
C
C     PRINT EXPECTED FREQUENCIES
C
C
      ITRIP=0
      WRITE(26,45)
884   ITRIP=ITRIP+1
      CALL IXOUT(MM,NN)
      WRITE(26,46)(I,I=NN,MM)
      DO 40 I=1,M
            WRITE(26,26)I,(EFL(I,J),J=NN,MM)
40    CONTINUE
      IF(M.GT.(ITRIP*10))GOTO 884
      WRITE(26,750)MTALLY
750   FORMAT(//10X,'NUMBER OF CELLS GT 0 BUT LT 1 =',I5)
      WRITE(26,751)ITALLY
751   FORMAT(//10X,'THE NUMBER OF CELLS GE 1 BUT LT 5=',I5)
      IF(KNT.EQ.0)GOTO 1343
      WRITE(26,752)((FLOAT(ITALLY+MTALLY))/(FLOAT(KNT))*100)
752   FORMAT(//10X,'% OF ALL NON ZERO CELLS LT 5 =',F8.2)
C
C
C
```

```
C       PRINT CHI SQUARE MATRIX
C
C
1343    ITRIP=0
        WRITE(26,47)
885     ITRIP=ITRIP+1
        CALL IXOUT(MM,NN)
        WRITE(26,46)(I,I=NN,MM)
        DO 50 I=1,M
               WRITE(26,26)I,(ECL(I,J)**2,J=NN,MM)
50      CONTINUE
        IF(M.GT.(ITRIP*10))GOTO 885
C
C
C
        DF=(M-1)*(N-1)
        WRITE(26,700)CHIT,DF
700     FORMAT(//10X,'OVERALL CHI SQUARE =',F10.3,' FOR df ='
       *,F5.0)
        WRITE(26,8111)
8111    FORMAT(3X,'FOR df LT 30, USE THE TABLE VALUES FOR
       * CRITICAL CHI SQUARE')
        IF(DF.LT.30)GOTO 4503
C
C
C
C       CALCULATE CRITICAL CHI SQUARE USING THE FORMULA
C       FOR Z-SCORE EQUIVALENTS OF CHI SQUARE
C
C
        INTRIP=0
3392    INTRIP=INTRIP+1
        IF(INTRIP.EQ.1)ZALPHA=1.645
        IF(INTRIP.EQ.1)ALPHA=.05
        IF(INTRIP.EQ.2)ZALPHA=2.236
        IF(INTRIP.EQ.2)ALPHA=.01
        IF(INTRIP.EQ.3)ZALPHA=3.090
        IF(INTRIP.EQ.3)ALPHA=.001
        ZASQ=ZALPHA**2
        PART2=2*(ZALPHA*(SQRT(2*(DF-1))))
        PART3=2*(DF-1)
        CRITCHI=(ZASQ+PART2+PART3)/2
        WRITE(26,3391)CRITCHI,ALPHA
3391    FORMAT(10X,'CRITICAL CHI SQ =',F10.2,' FOR ALPHA= ',
       *F8.3)
        IF(INTRIP.LT.3)GOTO 3392
4503    CONTINUE
45      FORMAT(///10X,'EXPECTED FREQUENCIES'//)
46      FORMAT(////4X,'START/FO',50I10///)
```

```
47      FORMAT(///10X,'CHI SQUARE VALUES'//)
26      FORMAT(7X,I5,50F10.3)
242     FORMAT(6X,'   TOT',50I10//)
230     FORMAT(/////10X,A5//)
C
C
        ITRIP=0
        WRITE(26,48)
48      FORMAT(////10X,'Y MATRIX WHERE Y=O-E/SQRT(E)'////)
890     ITRIP=ITRIP+1
        CALL IXOUT(MM,NN)
        WRITE(26,46)(I,I=NN,MM)
        DO 725 I=1,M
               WRITE(26,26)I,(ECL(I,J),J=NN,MM)
725     CONTINUE
        IF(M.GT.(ITRIP*10))GOTO 890
        WRITE(26,333)
333     FORMAT(///10X,'SIGNIFICANT TRANSITIONS')
        WRITE(26,343)
343     FORMAT(10X,'EVALUATED WITH 1 df AND REPERTOIRE
      * SIZE = 1')
        WRITE(26,701)
701     FORMAT(/10X,'USING THE FAGEN AND YOUNG (1978)
      *FORMULA')
        WRITE(26,702)
702     FORMAT(/10X,'i.e. /Y/ GT /SQRT(CHI SQ, 1df)/R**2/'//)
        WRITE(26,336)
336     FORMAT(/10X,'START/FOLL',15X,'CHI SQUARE')
        DO 334 I=1,M
               DO 334 J=1,N
                    IF(ABS(ECL(I,J).LT.1.959)GOTO 334
                    SIGN(I,J)='*   '
                    IF(ABS(ECL(I,J)).GE.2.575)SIGN(I,J)='** '
                    IF(ABS(ECL(I,J)).GE.3.290)SIGN(I,J)='***'
                    WRITE(26,335)I,J,ECL(I,J),SIGN(I,J)
335     FORMAT(10X,2I5,F10.3,A4)
334     CONTINUE
        WRITE(26,341)
341     FORMAT(//10X,'*= p LT .05/9X,'** = p LT .01/8X,
      *'*** = p LT .001'//)
        WRITE(26,250)
250     FORMAT(1H1)
C
C
C
C       CALL SUBROUTINE INFO TO COMPLETE ITA
C
C
        ITRIP=0
```

```
      CALL INFO
      X='PROB'
      WRITE(26,230)X
883   ITRIP=ITRIP+1
      CALL IXOUT(MM,NN)
      WRITE(26,46)(I,I=NN,MM)
      DO 800 I=M,N
            WRITE(26,26)I,(OPM(I,J),J=NN,MM),PRT(I)
800   CONTINUE
      WRITE(26,2111)(PCT(J),J=NN,MM)
      IF(M.GT.(ITRIP*10))GOTO 887
2111  FORMAT(A6X,'   TOT',50F10.3)
C
C
      WRITE(26,810)HMAX
810   FORMAT(//10X,'HMAX=',F10.5,'MAXIMUM INFORMATION
     * POSSIBLE IN THE ROW AND COLUMN DIMENSIONS:
     *((LOG10(R*C))*3.3219)'/)
      WRITE(26,811)H
811   FORMAT(10X,'H=',F10.5//)
      WRITE(26,812)HR
812   FORMAT(10X,'HR=',F10.5,'ESTIMATE OF THE INFO PRESENT
     * (UNCERTAINTY) IN THE ROW DIMENSION: BASED ON ROW
     * TOTALS'/)
      WRITE(26,813)HC
813   FORMAT(10X,'HC=',F10.5,' ESTIMATE OF THE INFO PRESENT
     * (UNCERTAINTY) IN THE COLUMN DIMENSION:  BASED ON
     * COLUMN TOTALS'/)
      WRITE(26,814)HRC
814   FORMAT(10X,'HRC=',F10.5,' ESTIMATE OF THE INFO IN THE
     * DYADS;  IF MANY EVENTS ARE COMMON AND FEW ARE RARE,
     * HRC IS HIGH'//)
      WRITE(26,815)HT
815   FORMAT(10X,'HT=',F10.5//)
      WRITE(26,816)HTP
816   FORMAT(10X,'HTP=',F10.5,'ESTIMATE OF INFO SHARED BY
     * ROW AND COLUMN DIMENSIONS;  A NORMALIZED H'/)
      WRITE(26,4001)
4001  FORMAT(10X,'VALUE THAT IS RELATIVELY UNBIASED BY
     * SAMPLE SIZE;  USEFUL IN MAKING COMPARISONS;  LOW
     * HTP'/10X,'MEANS COMMUNICATION EFFICIENCY --FEW
     * ACTIONS ARE NECESSARY TO GET A REACTION'/)
      WRITE(26,817)RI
817   FORMAT(10X,'RI=',F10.5/'HRC/HMAX;  TRANSMISSION
     * EFFICIENCY;  LOW RI SUGGESTS A SYSTEM CONTAINING
     * INFO (E.G. A NON-RANDOM ORGANIZATION)'/)
      WRITE(26,818)RED
818   FORMAT(10X,'RED=',F10.5//)
C
```

```
C
C
      CLOSE(UNIT=25)
      CLOSE(UNIT=26)
      STOP
      END
C
C
C
      SUBROUTINE INFO
C
C
C
C     SUBROUTINE TO CALCULATE INFORMATIONAL VALUES
C     ACCORDING TO INFORMATION THEORY ANALYSIS
C     SEE DUNHAM 1983 & 1984, LOSEY 1978, FENTRESS 1979
C
C
C
C     RETURNS OBSERVED PROBABILITY MATRIX (OPM) AND
C     VALUES FOR H TO THE CALLING PROGRAM
C
C
C
      COMMON MAT(50,50),LRT(50),LCT(50),LGT,EFL(50,50),
     *ECL(50,50),OPM(50,50),PRT(50),PCT(50),HMAX,H,
     *HR,HC,HRC,HT,HTP,RI,RED,M,N,ITRIP,ITALLY,CHIT,MTALLY,
     *KNT,SD,SRT(50),RPR(50),SCT(50),CPR(50),SIGMA(50,50),
     *A(50),B(50),ITER,NITER,DENOM,P(50,50),TD
      DIMENSION HH(50,50)
      DO 500 I=1,M
              IF(LGT.NE.0)PRT(I)=FLOAT(LRT(I))/FLOAT(LGT)
              DO 500 J=1,N
              IF(LGT.NE.0)PCT(J)=FLOAT(LCT(J))/FLOAT(LGT)
              IF(LGT.NE.0)OPM(I,J)=FLOAT(MAT(I,J))/FLOAT(LGT)
              IF(OPM(I,J).EQ.0)GOTO 500
                    IF(OPM(I,J).NE.0)AA=1/OPM(I,J)
                    HH(I,JJ)=ALOG10(AA)*3.3219
                    AA=0
500   CONTINUE
      AB=FLOAT(M*N)
      HMAX=(ALOG10(AB))*3.3219
      H=0
      HRC=0
      HC=0
      DO 513 I=1,M
              IF(PRT(I).EQ.0)GOTO 514
      HR=HR+(-(PRT(I)*(ALOG10(PRT(I))*3.3219)))
514   DO 510 J=1,N
```

```
              IF(MAT(I,J).EQ.0)GOTO 510
              H=H+(HH(I,J)*OPM(I,J))
              IF(OPM(I,J).EQ.)GOTO 510
              HRC=HRC+(-(OPM(I,J)*(ALOG10(OPM(I,J))*3.3219))
510     CONTINUE
513     CONTINUE
        DO 511 J=1,N
              IF(PCT(J).EQ.0)GOTO 511
              HC=HC+(-(PCT(J)*(ALOG10(PCT(J))*3.3219)))
511     CONTINUE
        HT=HR+HC-HRC
        IF(LGT.NE.0)HTP=HT-((M-1)*(N-1)/(1.3863*(FLOAT(LGT))))
        RI=H/HMAX
        RED=1-RI
        RETURN
        END
C
C
C
C
C       SUBROUTINE TO COMPUTE THE NORMAL CHI SQUARE
C
C
        SUBROUTINE NORMAL
C
C
        COMMON MAT(50,50),LRT(50),LCT(50),LGT,EFL(50,50),
       *ECL(50,50),OPM(50,50),PRT(50),PCT(50),HMAX,H,
       *HR,HC,HRC,HT,HTP,RI,RED,M,N,ITRIP,ITALLY,CHIT,MTALLY,
       *KNT,SD,SRT(50),RPR(50),SCT(50),CPR(50),SIGMA(50,50),
       *A(50),B(50),ITER,NITER,DENOM,P(50,50),TD
        CHIT=0
        ITALLY=0
        MTALLY=0
        KNT=0
        DO 666 I=1,M
              DO 666 J=1,N
         IF(LGT.NE.0)EFL(I,J)=FLOAT(LRT(I)*LCT(J))/FLOAT(LGT)
         IF(EFL(I,J).LT.5.AND.EFL(I,J).GE.1)ITALLY=ITALLY+1
         IF(EFL(I,J).LT.1.AND.EFL(I,J).GT.0)MTALLY=MTALLY+1
              IF(EFL(I,J).EQ.0)GOTO 666
              KNT=KNT+1
        IF(EFL(I,J).NE.0)ECL(I,J)=(FLOAT(MAT(I,J))-EFL(I,J))/
       *SQRT(EFL(I,J))
              CHIT=CHIT+ECL(I,J)**2)
666     CONTINUE
        RETURN
        END
C
```

```
C
C
C       SUBROUTINE NODIAG TO DO A CHI SQUARE ANALYSIS
C       ON MATRICES WITH ZEROS ON THE DIAGONAL USING
C       THE GOODMAN (1968, 1984) ITERATIVE PROCEDURE
C
C
        SUBROUTINE NODIAG
C
C
C
        COMMON MAT(50,50),LRT(50),LCT(50),LGT,EFL(50,50),
       *ECL(50,50),OPM(50,50),PRT(50),PCT(50),HMAX,H,
       *HR,HC,HRC,HT,HTP,RI,RED,M,N,ITRIP,ITALLY,CHIT,MTALLY,
       *KNT,SD,SRT(50),RPR(50),SCT(50),CPR(50),SIGMA(50,50),
       *A(50),B(50),ITER,NITER,DENOM,P(50,50),TD
        SD=100
        DO 775 I=1,M
                SRT(I)=0
               IF(LGT.NE.0)RPR(I)=(FLOAT(LRT(I)))/(FLOAT(LGT))
                DO 775 J=1,N
                      SCT(J)=0
               IF(LGT.NE.0)CPR(J)=(FLOAT(LCT(J)))/(FLOAT(LGT))
                      SIGMA(I,J)=1
                      IF(I.EQ.J)SIGMA(I,J)=0
775     CONTINUE
        DO 776 I=1,M
                DO 776 J=1,N
                      SRT(I)=SRT(I)+SIGMA(I,J)
                      SCT(J)=SCT(J)+SIGMA(I,J)
776     CONTINUE
C
C
C       INITIALIZE A1 ETC
C
C
        DO 630 I=1,M
                DENOM=0
                DO 625 J=1,N
                      DENOM=DENOM+(B(J)*SIGMA(I,J))
625             CONTINUE
                IF(DENOM.NE.0)A(I)=RPR(I)/DENOM
630     CONTINUE
        DENOM=0
C
C
C       INITIALIZE PREDICTED PROBABILITY MATRIX AND
C       FILL WITH VALUES P(I,J)=A(I)*B(J)
C
```

```
C
      DO 640 I=1,M
            PRT(I)=0
            DO 640 J=1,N
                PCT(J)=0
                P(I,J)=0
640   CONTINUE
      DO 641 I=1,M
            DO 641 J=1,N
                P(I,J)=A(I)*B(J)
                IF(I.EQ.J)P(I,J)=0
                PRT(I)=PRT(I)+P(I,J)
                PCT(J)=PCT(J)+P(I,J)
641   CONTINUE
C
C
C     CHECK FOR DIFFERENCES BETWEEN ORIGINAL ROW AND
C     COLUMN PROPORTIONS AND THOSE FOR PREDICTED
C     PROBABILITY MATRIX.  IF THE SUM OF THE DIFFERENCES
C     IS GT /.00001/ AND FEWER THAN THE SPECIFIED NUMBER
C     OF ITERATIONS HAVE OCCURRED, GO BACK TO COMPUTE NEW
C     VALUES FOR A AND B AT LINE 605.
C
C
C     CONVERGENCE CRITERION IS .00001
C
C
C     OTHERWISE COMPUTE EXPECTED FREQUENCIES AND COMPLETE
C     CHI SQUARE
C
C
      TD=0
      DO 6000 I=1,M
            DO 6000 J=1,N
                TD=TD+(RPR(I)-PRT(I))
                TD=TD+(CPR(J)-PCT(J))
6000  CONTINUE
      IF(TD.LT.SD)SD=TD
      WRITE(26,6057)
6057  FORMAT(10X,'CONVERGENCE CRITERION IS .00001')
      WRITE(26,6001)ITER,SD
6001  FORMAT(1H ,10X,'DIFFERENCE AFTER',I5,' ITERATION(S)
     * IS',F15.10)
      IF(SD.GT..00001)GOTO 605
C
C
C     COMPUTE EXPECTED MATRIX
C
C
```

```
3199    CHIT=0
        ITALLY=0
        MTALLY=0
        KNT=0
                DO 714 I=1,M
                DO 714 J=1,N
         EFL(I,J)=P(I,J)*FLOAT(LGT)
         IF(EFL(I,J).LT.5.AND.EFL(I,J).GE.1)ITALLY=ITALLY+1
         IF(EFL(I,J).LT.1.AND.EFL(I,J).GT.0)MTALLY=MTALLY+1
                IF(EFL(I,J).LE.0)GOTO 714
                KNT=KNT+1
        IF(EFL(I,J).NE.0)ECL(I,J)=(FLOAT(MAT(I,J))-EFL(I,J))/
       *SQRT(EFL(I,J))
                CHIT=CHIT+ECL(I,J)**2)
714     CONTINUE
        GOTO 720
700     WRITE(26,701)NITER
701     FORMAT(1H ,10X,'CONVERGENCE NOT ACHIEVED ON',I5,
       *' ITERATIONS')
        GOTO 3199
720     RETURN
        END
C
C
C
C       SUBROUTINE TO FORMAT OUTPUT MATRICES TO
C       10-COLUMN FORMAT
C
C
C
        SUBROUTINE IXOUT(MM,NN)
C
C
C
        COMMON MAT(50,50),LRT(50),LCT(50),LGT,EFL(50,50),
       *ECL(50,50),OPM(50,50),PRT(50),PCT(50),HMAX,H,
       *HR,HC,HRC,HT,HTP,RI,RED,M,N,ITRIP,ITALLY,CHIT,MTALLY,
       *KNT,SD,SRT(50),RPR(50),SCT(50),CPR(50),SIGMA(50,50),
       *A(50),B(50),ITER,NITER,DENOM,P(50,50),TD
        IF(ITRIP.EQ.1)THEN
                NN=1
                MM=10
                IF(M.LT.10)MM=M
        ELSE IF(ITRIP.EQ.2)THEN
                NN=11
                MM=20
                IF(M.LE.20)MM=M
        ELSE IF(ITRIP.EQ.3)THEN
                NN=21
```

```
            MM=30
            IF(M.LE.30)MM=M
            ELSE IF(ITRIP.EQ.4)THEN
            NN=31
            MM=40
            IF(M.LE.40)MM=M
      ELSE IF(ITRIP.EQ.5)THEN
            NN=41
            MM=M
      END IF
      RETURN
      END
C
C
C
```

APPENDIX C

```
C
C
C
C     FORTRAN PROGRAM TO COMPLETE A LAG SEQUENCE ANALYSIS
C
C                     BY LINDA SORENSEN
C
C                       APRIL 1985
C
C
C     EVENT LAG - MAX LAG 15
C     FORMATTED FOR BABY DATA
C     IN THE FILE BDATA2.SET
C
C     HANDLES ANY NUMBER OF SEQUENCES OF ANY LENGTH
C     FOR UP TO 50 DIFFERENT BEHAVIOR CODES
C
C
C
C     REVISE  IEND TO EQUAL END OF SESSION CODE OR END
C     OF SEQUENCE CODE AS APPROPRIATE
C
C
C
C     SUBROUTINE CRIT ESTABLISHES THE RANGE OF CRITERION
C     BEHAVIORS (MAX 50)
C
C     THE DO LOOP AT 2010 ESTABLISHES THE RANGE OF FOLLOW
C     BEHAVIORS (MAX 50)
C
C     THE DO LOOP AT 2020 ESTABLISHES THE RANGE OF LAGS
C     (MAX 15)
C
C
C
C     THE PROGRAM MUST BE REVISED TO SPECIFY THE INPUT FILE
C     (UNIT=16)
C     AND THE OUTPUT FILE FOR THE LAG DATA (UNIT=15)
C     AND THE OUTPUT FILE FOR THE LAG PLOTS (UNIT=17)
C
C
C
C     AFTER SACKETT 1978 AND 1979
C
C
C
C     PROGRAM MUST BE REVISED IF EACH BEHAVIOR CANNOT
```

```
C      FOLLOW ITSELF IN THE DATA SET -- SEE SACKETT
C      1979 PAGE 637
C
C
C
       COMMON PLMAT(250,16),AM,AN
       DIMENSION IB(16),AOP(50),P(50,15),LAG(50,15),KNT(50),
      *ICT(15),PEXP(50,15),SDE(50,15),Z(50,15),UCI(50,15),
      *ULCI(50,15),WARN(50,15),AAA(15),SIG(50,15)
       OPEN(UNIT=15,FILE='ACTALL.LAG')
       OPEN(UNIT=16,FILE='ACTALL.PLT')
       OPEN(UNIT=17,FILE='BDATA2.SET')
C
C
C
       IEND=49
C
C
C
       ICNT=0
402    CALL CRIT(ICB,ICNT,MICNT)
       DO 15 I=1,16
            IB(I)=0
15     CONTINUE
       DO 20,I=1,50
            KNT(I)=0
            AOP(I)=0
                 DO 20 J=1,15
                      ICT(J)=0
                      SIG(I,J)='    '
                      LAG(I,J)=0
                      P(I,J)=0
20     CONTINUE
       KTOT=0
       IICT=0
C
C
111    DO 100 I=1,16
            READ(16,105,END=305)IB(I)
105         FORMAT(35X,I2)
            KNT(IB(I))=KNT(IB(I))+1
100    CONTINUE
C
C
C
110    IF(IB(I).NE.ICB)GOTO 200
       K=1
       DO 150 L=2,16
            LAG(IB(L),K)=LAG(IB(L),K)+1
```

```
            K=K+1
C
C
C
      IF(IB(L).GE.IEND)GOTO 200
C
C
C
150   CONTINUE
200   IF(K.EQ.2)GOTO 111
      DO 210 J=1,15
            IB(J)=IB(J+1)
210   CONTINUE
C
C
      READ(16,105,END=305)IB(16)
      KNT(IB(16))=KNT(IB(16))+1
      GOTO 110
C
C
305   DO 300 I=1,50
            KTOT=KTOT+KNT(I)
300   CONTINUE
C
C
      DO 310 I=1,50
            DO 310 J=1,15
                  ICT(J)=ICT(J)+LAG(I,J)
310   CONTINUE
      DO 2007 J=1,15
            IICT=IICT+ICT(J)
2007  CONTINUE
C
C
C
      DO 350 I=1,50
            IF(KTOT.EQ.0)GOTO 343
            AOP(I)=(FLOAT(KNT(I)))/(FLOAT(KTOT))
            GOTO 344
343         AOP(I)=0.0
344         DO 360 J=1,15
                  IF(ICT(J).EQ.0)GOTO 355
                  P(I,J)=(FLOAT(LAG(I,J)))/(FLOAT(ICT(J)))
                  GOTO 360
355               P(I,J)=0.0
360         CONTINUE
350   CONTINUE
C
C
```

```
      IF(KTOT.EQ.0)GOTO 402
C
C
      WRITE(15,400)ICB
400   FORMAT('0',///'CRITERION BEHAVIOR IS:',I3)
      WRITE(15,410)
410   FORMAT('0',33X,'EVENT LAG -- MAX LAG 15')
      WRITE(15,420)
420   FORMAT('0',15X,'FREQUENCY AT EACH LAG',55X,
     *'OBSERVED PROBABILITY')
      WRITE(15,430)(J,J=1,15),(K,K=1,15)
430   FORMAT('0','BEH',2X,'A',2X,15I4,7X,7X,'B',2X,
     *5I5,2(/87X,5I5)
C
C
C
      DO 440 I=1,50
           IF(KNT(I).EQ.O)GOTO 440
           WRITE(15,1100)I,KNT(I),(LAG(I,J),J=1,15),AOP(I)
     *,(P(I,J),J=1,15)
1100  FORMAT(' ',I2,I4,2X,15I4,10X,F6.1,2X,5F5.1,2(/87X,
     *5F5.1))
440   CONTINUE
      WRITE(15,1101)KTOT,(ICT(J),J=1,15)
1101  FORMAT(' ',I6,2X,15I4)
C
C
      WRITE(15,460)
460   FORMAT('0','A=OVERALL FREQUENCLY IN DATA'/'0',
     *'B=PROPORTION OF ALL BEHAVIOR CHANGES'/'1')
C
C
C
C     COMPUTE Z SCORES AND 95% CONFIDENCE INTERVALS
C     FOR EVENT LAGS 1 TO 15 FOR EACH CRITERION BEHAVIOR
C     AND EACH MATCHING BEHAVIOR
C
C
      DO 1000 I=1,50
           DO 1000 J=1,15
                IF(KNT(I).EQ.0)GOTO 1000
      PEXP(I,J)=(FLOAT(ICT(J))/(FLOAT(KNT(I)))*AOP(I)))
1000  CONTINUE
      DO 2000 I=1,50
           DO 1010 J=1,15
                WARN(I,J)='  '
                IF(ICT(J).LT.30)WARN(I,J)='++'
                IF(PEXP(I,J).LT..05)WARN(I,J)='++'
                IF(ICT(J).EQ.0)GOTO 1160
```

```
                 SDE(I,J)=SQRT((PEXP(I,J)*(1-PEXP(I,J)))/
     *(FLOAT(ICT(J))))
                 IF(SDE(I,J).EQ.0)GOTO 1160
                 Z(I,J)=(P(I,J)-PEXP(I,J))/SDE(I,J)
                 GOTO 1164
1160             SDE(I,J)=0
                 Z(I,J)=0
1164             UCI(I,J)=PEXP(I,J)+(1.96*SDE(I,J))
                 ULCI(I,J)=PEXP(I,J)-(1.96*SDE(I,J))
                 IF(Z(I,J).GE.1.96)SIG(I,J)='*'
                 IF(Z(I,J).LE.-1.96)SIG(I,J)='*'
                 IF(Z(I,J).GE.2.515)SIG(I,J)='**'
                 IF(Z(I,J).LE.-2.515)SIG(I,J)='**'
                 IF(Z(I,J).GE.3.290)SIG(I,J)='***'
                 IF(Z(I,J).LE.-3.290)SIG(I,J)='***'
1010         CONTINUE
2000  CONTINUE
      WRITE(15,2001)
2001  FORMAT(' '///,20X,'Z SCORES AND CONFIDENCE
     *INTERVALS'//)
      WRITE(15,2002)
2002  FORMAT(3X,'CRIT',1X,'FOLL BY',1X,'AT LAG=',6X,'Z=',7X,
     *5X,'LCI=',7X,'UCI=')
C
      DO 2010 I=1,50
C
C
C
      CALL INIT
C
C
      IF(KNT(I).EQ.0)GOTO 2010
C
          DO 2020 J=1,15
C
      IF(UCI(I,J).GT.UCI(I,J+1))UCI(I,J)=UCI(I,J+1)
      WRITE(15,2030)ICB,I,J,Z(I,J),SIG(I,J),ULCI(I,J),
     *UCI(I,J),WARN(I,J)
2030  FORMAT(3X,I4,1X,I7,1X,I6,F10.1,A3,6X,F6.1,6X,F6.1,A3)
      IF(UCI(I,J).GT.AM)AM=UCI(I,J)
      IF(P(I,J).GT.AM)AM=P(I,J)
      IF(ULCI(I,J).LT.AN)AN=ULCI(I,J)
      IF(P(I,J).LT.AN)AN=P(I,J)
2020  CONTINUE
      AM=AM+.02
      AN=AN-.02
      M=IFIX(AM*100)
      N=IFIX(AN*100)
      IIJ=M+IABS(N)+1
```

```
      DO 570 J=1,15
            JLAG=J+1
            L=IFIX(P(I,J)*100)
            L=L+IABS(N)+1
            PLMAT(L,JLAG)=' .'
            LL=IFIX(ULCI(I,J)*100)
            LL=LL+IABS(N)+1
            IF(LL.EQ.L)THEN
                  PLMAT(LL,JLAG)=' *'
            ELSE
                  PLMAT(LL,JLAG)=' -'
            ENDIF
            LLL=IFIX(UCI(I,J)*100)
            LLL=LLL+IABS(N)+1
            IF(LLL.EQ.L)THEN
                  PLMAT(LLL,JLAG)=' *'
            ELSE
                  PLMAT(LLL,JLAG)=' -'
            ENDIF
570   CONTINUE
      WRITE(17,560)ICB,I
560   FORMAT((/////5X,'CRITERION BEHAVIOR IS:',I5/10X,
     *'MATCH BEHAVIOR IS:',I5//)
      WRITE(15,561)
561   FORMAT(8X,'OBSERVED PROBABILITY'/)
      DO 510 II=M,N,-1
            IF(II.GT.100)GOTO 1847
            WRITE(17,520)II,(PLMAT(IIJ,IJLAG),IJLAG=1,16)
520         FORMAT(10X,I3,16A2)
1847        IIJ=IIJ-1
510   CONTINUE
      DO 550 IJ=1,32
            AAA(IJ)='+'
550   CONTINUE
      WRITE(17,530)(AAA(JJ),JJ=1,31),(LLAG,LLAG=1,15)
530   FORMAT(14X,31A1/15X,15I2)
      WRITE(17,531)
531   FORMAT(28X,'LAG')
2010  CONTINUE
      WRITE(15,2111)
2111  FORMAT(' '///,5X,'++  WARNING: TOTAL LAG FREQUENCY OR
     *PEXPECTED IS TOO SMALL FOR THE BINOMIAL TEST'//)
      WRITE(15,2112)
2112  FORMAT(' ',5X,'*   SIGNIFICANT AT THE .05 LEVEL'/,
     *5X,'**  SIGNIFICANT AT THE .01 LEVEL'/,
     *5X,'*** SIGNIFICANT AT THE .001 LEVEL'///)
      CLOSE(UNIT=16)
      IF(ICNT.EQ.MICNT)GOTO 977
      GOTO 402
```

```
977    CLOSE(UNIT=15)
       CLOSE(UNIT=17)
       STOP
       END
C
C
C
       SUBROUTINE INIT
       COMMON PLMAT(250,16,AM,AN
       AM=-90
       AN=90
       M=0
       N=0
       L=0
       LL=0
       LLL=0
       IIJ=0
       DO 500 I=1,250
            DO 500 J=1,16
                 PLMAT(I,J)='   '
                 IF(J.EQ.1)PLMAT(I,J)=' +'
500    CONTINUE
       RETURN
       END
C
C
C
       SUBROUTINE CRIT(ICB,ICNT,MICNT)
       ICNT=ICNT+1
       IF(ICNT.EQ.1)ICB=23
       IF(ICNT.EQ.2)ICB=24
       IF(ICNT.EQ.3)ICB=25
       IF(ICNT.EQ.4)ICB=27
       IF(ICNT.EQ.5)ICB=31
       IF(ICNT.EQ.6)ICB=32
       IF(ICNT.EQ.7)ICB=33
       IF(ICNT.EQ.8)ICB=34
       IF(ICNT.EQ.9)ICB=35
       IF(ICNT.EQ.10)ICB=36
       IF(ICNT.EQ.11)ICB=38
       IF(ICNT.EQ.12)ICB=41
C
C
C      SET MICNT EQUAL TO MAX ICNT (SPECIFIED IN PREVIOUS
C      LINE
C
C
       MICNT=12
C
```

```
C
C
      RETURN
      END
```

APPENDIX D

Shown on the following pages are two tables which include the factor loadings and transition matrices for the non-symmetric multidimensional scaling solutions. The first table gives details associated with Figure 6 and the second information that pertains to Figure 8. Each table is divided into two parts; the upper part of the table gives the factor loadings and the lower part gives the transition frequencies. The transition frequencies can be interpreted in the same units as the raw data.

Table 1. Shown below are the factor loadings and transition frequencies associated with Figure 6.

ACTIVITY	DIMENSION 1	2	3	4
EAT	.01	.04	.18	-.03
DRINK	.02	.88	.03	.02
CARRY	.05	-.02	.05	-.03
SELF GROOM	.04	.02	.07	.74
WALK	.15	-.16	.10	.24
RUN	.61	-.15	-.05	.17
IMMOBILE	-.05	.25	.14	.01
LEDGE DOWN	.70	.13	.00	-.11
SCRATCH/DIG	-.01	-.02	.94	.01
LEDGE UP	.13	.03	-.07	.08
NESTBOX	.01	.18	-.02	.02
URINATE/DEFECATE	-.11	.06	-.09	.57
HEAD-IN-TUBES	.05	.07	.00	.02
RUB/SCRATCH/SNIFF	-.00	.12	.10	.01
SCENT MARK	-.07	.18	-.00	.09
SOCIAL	.24	.11	.10	-.11

DIMENSION	DIMENSION 1	2	3	4
1	1755	1799	560	624
2	1673	881	402	2673
3	550	559	2636	697
4	472	2256	905	2010

Table 2. Shown below are the factor loadings and transition frequencies associated with Figure 8.

ACTIVITY	DIMENSION 1	2	3
EAT	.59	-.05	-.01
LEDGE	.54	-.07	.00
SCRATCH/DIG	.46	.04	-.04
SCENT MARK	.24	.04	.05
SNIFF	.05	.25	-.01
PAW	-.01	.15	.17
WALK OVER	.04	.28	.01
STAND OVER	-.02	.13	.12
REST IN CONTACT	-.06	.64	-.06
BITE	-.03	-.03	.47
ALLOGROOM	-.01	.09	-.01
MUTUAL GROOM	-.02	.13	-.03
LATERAL PUSH	.00	.07	.11
CLASP	-.02	.04	.28
BIPEDAL CLASP	-.00	-.12	.45
HEAD FENCE	-.02	-.03	.37
POUNCE	-.00	-.01	.29
CHASE	.02	-.07	.26
INVESTIG. GENITALS	-.05	.42	-.01
DART	.00	.04	.26
EN FACE	.13	.08	.17

DIMENSION	DIMENSION 1	2	3
1	8831	2146	366
2	1910	4251	966
3	472	819	1062

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