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RESEARCH ARTICLE

Describing the Organization of Dominance Relationships by Dominance-Directed Tree Method

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Methods to describe dominance hierarchies are a key tool in primatology studies. Most current methods are appropriate for analyzing linear and near-linear hierarchies; however, more complex structures are common in primate groups. We propose a method termed ''dominance-directed tree.'' This method is based on graph theory and set theory to analyze dominance relationships in social groups. The method constructs a transitive matrix by imposing transitivity to the dominance matrix and produces a graphical representation of the dominance relationships, which allows an easy visualization of the hierarchical position of the individuals, or subsets of individuals. The method is also able to detect partial and complete hierarchies, and to describe situations in which hierarchical and nonhierarchical principles operate. To illustrate the method, we apply a dominance tree analysis to artificial data and empirical data from a group of *Cebus apella*. Am. J. Primatol. 68:189–207, 2006. © 2006 Wiley-Liss, Inc.

Key words: dominance hierarchy, graph theory, social structure, Cebus

INTRODUCTION

The concept of dominance hierarchy has been considered a central feature for understanding the organization of primate social groups. Dominance is defined as the attribute of repeated patterns of agonistic interactions between two individuals, such that dominants win most of the conflicts over subordinate individuals [Drews, 1993]. If individuals of a social group can be ordered based on dominance relationships, then a dominance hierarchy is present. The concept is very appealing because the complexities of the social relationships can be

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summarized by a reduced set of relationships or by some simple rules as given by the hierarchical principles.

However, the term ''hierarchy'' has been loosely used in behavioral studies and may have contradictory meanings. It is not true that any set of dominance relationships forms a hierarchy [Drews, 1993]. Moreover, lack of linearity is not synonymous with nonhierarchical dominance relationships. This mistaken assumption is probably related to the fact that nearly all current methods of studying dominance structure are based on the linear hierarchical model, either by calculating an index of linearity or by ordering individuals of a social group into linear or near-linear dominance hierarchies [reviewed in de Vries, 1998; de Vries & Appleby, 2000].

However, primates may present more complex dominance relationships, organized into partial hierarchies with several independent branches, that are not properly assessed by current methods [Jameson et al., 1999].

In the present work we propose the use of set theory and the graph theory concept of directed tree as a more general method for describing dominance organization. We begin with a formal definition of structure and hierarchy with the aid of set and graph theories, and suggest that the number of individuals restricts the type of organization and the type of hierarchy that may arise in the social structure. We illustrate the method (here called dominance tree analysis) by analyzing hypothetical data sets that were devised to mimic the complexities generally found in real data, and provide an example using field data from *Cebus apella*.

The use of formal terms is by no means standard in set theory and graph theory. Thus, explicit definitions and notations are needed. Whenever possible, we adapted the formal terms to those customarily used in the study of social groups (see Pinter [1971] and Pollock [1990] for expositions of set theory, and Harary et al. [1965] and Carley and Prietula [1994] for graph theory)

MATERIALS AND METHODS

Structures and Hierarchy

In this work a social structure is defined by a nonempty set of members (the individuals of a social group) and a set of dyadic dominance relationships (a binary relation on the set of members). So defined, the structure is a graph, as defined in graph theory. The number of members (here denoted by N) defines the size of the structure. For simplicity, here ''relation'' refers only to dominance relationships, and covers different types of relationships (overt aggression, threatening, displacement of the opponent, priority of access to food or females, etc.).

To conform to the concept of structure, dominance should be stated as a binary relation within the set of members. We denote the dominance relationship by the ''greater than'' sign (e.g., A > B means ''A dominates B'' or ''A defeats B'').

A structure may be represented by a matrix of dominance relationships in which the cells take a value of one if the row member dominates the column member, or zero if the row member does not dominate the column member. We denote the cell of the row member A and column member B as [A,B], and, for simplicity, its value as [A,B] = 1 if individual A dominates individual B, or [A,B] = 0 if A does not dominate B. A general cell is denoted by letters in italics, e.g., $[i,j]$. By definition, every dominance matrix has the property of irreflexivity (for every member i, $[i,i] = 0$) and asymmetry (for all different members i and j, if $[i,j] = 1$, then $[j,i] = 0$). It is not necessary for all dyads to show dominance relationships, so it is possible that, for some dyads, $[i,j] = 0$ and $[j,i] = 0$.

Orders

A structure is said to be an order if in addition to irreflexivity and asymmetry, it has the property of *transitivity*: for every members i, j and k, if $i>j$ and $j>k$, then $i>k$. Or, in terms of the matrix notation, if $[i,j] = 1$ and $[j,k] = 1$, then $[i,k] = 1$. A structure fails to be transitive (and hence is not an order) if there exist members i, j, and k such that $[i,j] = 1$, $[j,k] = 1$, but $[i,k] = 0$. A severe failure of transitivity occurs when the structure shows circular triads: for some i, j, and k, $i>j$, $j>k$, and $k>i$.

In this work "hierarchy" is defined as an order. Hence, a hierarchy is a structure that is irreflexive, asymmetric, and transitive. Irreflexivity and asymmetry result directly from the definition of the dominance relationship. Transitivity should be checked in each case.

Hierarchies may be linear or partial.

Linear Hierarchy

A linear hierarchy is a structure that in addition to being an order, is also complete: for every different pair i and j, $[i,j] = 1$ or else $[j,i] = 1$. Therefore, we need to assess the dominance relationship in all possible dyads, as in a round-robin tournament. Thus, the number of nonzero dominance relationships is given by $N(N-1)/2$. In terms of set theory, we say that every two members show comparability in respect to the dominance relation.

It is very easy and simple to describe a complete order. All of the relevant information is given by a unique ordered arrangement of the members—for example, A>B>C>D>E in a group of five members. Here we call this type of ordered arrangement a lineage. Only $N-1$ relationships (those relating two adjacent members in the lineage (four, in the example above)) are relevant to describe the hierarchy. The other relationships are given by the transitive property: if A>B and B>C, then in a linear hierarchy we also have A>C. So, by using only the $N-1$ relevant relationships and the transitive property, we retrieved the totality of the $N\,(N-1)/2$ relationships of the dominance matrix. An example of a complete order is a set of real numbers, in which each pair of numbers is related by the "greater than" relation.

The concept of linear hierarchy is customarily found in studies of the dominance relationships of small structures [Drews, 1993]. The concept is still useful if the departures from linearity, as caused by circular triads, nontransitivity, or noncomparability between two members, are small. These departures may be measured and statistically tested (for statistical methods see Appleby [1983] and de Vries [1995]).

A small index of linearity means a low degree of *linear* hierarchy, but it does not mean the absence of hierarchy. Another type of hierarchy, called partial hierarchy, may be in operation.

Partial Hierarchy

The requirement of completeness restricts the use of the linear hierarchy model to small groups. It is practically impossible to obtain completeness among members of a large group of, say, 200 individuals. Temporal limitations prevent the sampling of a sufficient amount of dominance relationships. Even when it is possible to gather a sufficient amount of dominance relationships, the structure is not expected to be the same after the long period of time needed to gather all of the dominance relationships has passed.

A hierarchy that is not complete is called a partial hierarchy. Therefore, given that some dyads are not comparable, the total amount of dominance relationships is smaller than $N(N-1)/2$. In a partial hierarchy, we cannot graphically display all of the members in a unique lineage. Partial hierarchies may be of two types depending on the number of relevant relationships needed to describe the partial hierarchy.

In the first type, the number of relevant dominance relationships is still equal to $N-1$, but they are distributed in at least two lineages that emerge from a common member. Suppose, for example, that the relevant relationships are given by the two lineages A>B>C and A>B>D>E. In each lineage, each member is comparable to the other. Except for the common members, members from distinct lineages do not show comparability. The common members of these two lineages are A and B. The relationship A>B appears in the two lineages. If we eliminate the redundancy by discarding the relationship A>B from one lineage, we may describe the partial hierarchy by A>B>C and B>D>E or, equivalently, by B>C and A>B>D>E, so that the amount of relevant relationships is still $N-1$. A particular example of a partial hierarchy with $(N-1)$ relevant relationships is the despotic hierarchy (i.e., one member dominates the others and no dominance relationship exists among the other members [Wilson, 1975]). A despotic hierarchy may be represented by a radial display, with the dominant member at the center and generating several lineages, that reflects the relevant relationships (four dominance relationships, A>B, A>C, A>D, A>E, in a group of five members, with A being the despotic member).

In the second type, the number of relevant relationships is less than $N-1$; that is, there are at least two independent lineages. For example, a partial hierarchy with five members may be formed by the two independent lineages A>B>C and D>E. Note that the number of relevant relationships is smaller than $N-1$ (in this example, three instead of four).

Distinguished Members in a Hierarchy

Ordered sets have distinguished elements. For a hierarchical structure, the corresponding distinguished members are as follows (the corresponding names in set theory are in parentheses):

The *dominant member* (last element) dominates every member in the structure. A hierarchy has at most one dominant member. A dominant member only exists in linear hierarchies and in partial hierarchies where all lineages begin at the dominant member.

The *partial-dominant member* (maximal element) is not dominated by any member of the structure. The single partial-dominant member of a structure is also the dominant member, but partial hierarchies may have more than one partial-dominant member (for example, two in a structure with two independent lineages). In this case, the structure has several partial-dominant members but no dominant member.

The *subordinate member* (first element) is dominated by every member of the structure. Like the dominant member, the subordinate member (if there is one) is unique. This type of dominance relationship occurs in linear hierarchies or in partial hierarchies in which all lineages end at the subordinate member.

The *partial-subordinate member* (minimal element) does not dominate any member of the structure. The single partial-subordinate member of a structure is also the subordinate member, but partial hierarchies may have more than one partial-subordinate member. In this case, the structure has several partial-subordinate members but no subordinate member.

Assumption of Transitivity

In large structures, it is biologically unrealistic to expect that the ''dominant'' member should fight against all the other members of the group. In this case, we have to imply transitivity to try to uncover its hierarchical nature. That is, given the observed dominant relationships $A>B$, $B>C$, $C>D$, etc., but not necessarily $A>C$, or $A>D$, or $B>D$, etc., we simply force the structure to be transitive by implying $A>C$, $A>D$, $B>D$, etc. After the assumption of transitivity is applied repeatedly until no more changes occur, the modified dominance matrix is called the transitive closure graph (here the transitive matrix). Therefore, the assumption of transitivity may distort the dominance matrix by introducing extra dominance relationships. We can evaluate the severity of the distortion by analyzing the quantity and nature of the extra dominance relationships.

The assumption of transitivity states simply that if [A,B] = 1 and [B,C] = 1, we have to make [A,C] = 1, whatever may be the observed value of [A,C]. If this value is already 1 (that is, transitivity already holds), no information is added to the dominance matrix. If the value is zero, however, the severity of the distortion depends on the value of [C,A]. In the simplest case in which [C,A] is also zero, the only distortion is that we force the structure to be transitive. If, however, [C,A] = 1, a circular triad occurs, and then the transitive matrix fails to be asymmetric and irreflexive. It fails to be asymmetric because [A,C] = 1 and [C,A] = 1. Furthermore, it fails to be irreflexive because [A,A] = 1 (under the assumption of transitivity, if [A,C] = 1 and [C,A] = 1, then [A,A] = 1).

Treatment of Ties

Dominance matrices are constructed from the observed contests between any two members. In general, the decision as to which member is the winner and which is the loser is based on the net result of the contests. However, ties may occur.

There are three types of ties to the points discussed here: zero ties, low-value ties, and high-value ties. The definition of structure given above admits zero ties. However, nonzero ties must be managed somehow to preserve the property of asymmetry.

Zero Ties

Zero ties occur when there exist members i and j such that [i,j] = 0 and [j,i] = 0. Zero ties may occur by insufficient or biased sampling (in which cases the only recommendation is to correct the sampling procedure), or by the absence of dominance relationships. In the second case, a zero tie is a real phenomenon resulting from the impossibility of the members interacting (due, e.g., to physical distance or to formal impediments), from their unwillingness to contest (e.g., between a mother and her juveniles in some primate groups), or from any unknown avoidance strategy adopted by one or another member. In this work, all zero ties are treated as observational zeros (see also de Vries [1995]).

Low-Value Ties

Some pairs of members may show relatively low-value ties (say, one). We may consider these low values as reflecting only fortuitous and rare encounters that supposedly do not represent the general and regular absence of the dominance relationships that characterize the interaction between the members of the pair. In this case, a clearer and simpler account of the social structure may be obtained by setting these low values to zero.

We may extend the argument to cover those cases in which the dominance is established with relatively low values (say, 1×0). However, to define how relatively low these values are, and to evaluate the consequences of zero ties, a deeper analysis of each specific empirical dominance matrix is needed.

High-Value Ties

The occurrence of high-value ties is not expected in social structures in which dominance relationships are well established. High-value ties may occur in some transient phases of the dominance process (e.g., as a consequence of the group splitting or the introduction of new members), the high values resulting from a temporary escalation in the contests for hierarchical position. These conditions of unstableness generally cannot be satisfactorily dealt with by any method for describing structures (but see Broom [2002]). If a high-value tie is encountered, one has to decide the direction of the dominance relationship by using other kinds of information or collecting additional data. Obviously, since high values reflect contests for position in the social structure, they cannot be simply set to zero.

Dominance Trees

Lineages such as $A>B>C>D$ are easily represented in hierarchical diagrams as, say, $A \rightarrow B \rightarrow C \rightarrow D$. The specific member of the structure chosen to begin all lineages is called the root (A, if the lineage in the example is unique). A linear hierarchy is represented by a unique lineage beginning at the dominant member and ending at the subordinate member. For example, suppose the hierarchy is partial and has the second lineage $A \rightarrow B \rightarrow E \rightarrow F$. Both arrangements may be represented in a single directed tree diagram that bifurcates at B. The common parts of the paths are represented collectively as $A \rightarrow B$ and, emerging from B, the substructures $C \rightarrow D$ and $E \rightarrow F$.

Before we discuss this type of representation further, we will review some graph theory concepts that are useful for understanding dominance structures.

Paths in Dominance Structures

We have said that a dominance structure is a graph. We refer to a dominance structure as an elementary path (or path, for short) as an ordered arrangement of members, such as $A \rightarrow B \rightarrow C \rightarrow D$, in which no member is repeated. The members of a path are related by the reachability relation. In the example above, we may say that A reaches the other four members, C reaches D, D is reached from A, etc. Therefore, reachability is a one-way relationship from higher members of the hierarchy to lower ones, i.e., reachability is a relation in which transitivity holds.

If the substructure represented by a given path is hierarchical, then by definition no hierarchically lower member reaches a higher member. In contrast, if we assume that the members of the path are involved in circular triads, then by designating each member as the root, every member reaches and is reached by other members of the substructure. In this case, the structure is not hierarchical at all.

Dominance Tree Representation

A given path encloses all information contained in its subpath. For example, the information contained in the path B→C→D is already contained in the augmented path A→B→C→D→E. Thus, to get the maximum path information and eliminate redundancies, only the maximal paths are represented in the dominance tree. All information about direct dominance relations, such as A→D, are already encompassed in the maximal path and are skipped in the dominance tree.

The tree representation of all non-redundant maximal paths from a given member R is called the dominance tree of R. Given the dominance tree of R, the reachability relation can be used to construct a matrix based on the reachability relation. We call this the tree-dominance matrix of R. The importance of a member in the structure is given by the number of relationships in the transitive matrix that is explained by its tree-dominance matrix. For example, the tree-dominance matrix of the dominant member is identical to the transitive matrix.

Reduced Graph

Suppose that A dominates all the others, B dominates all the others except A, and that C, D, and E are involved in circular triads (for example, C > D, D > E, and E > C). The best dominance tree (that for member A) has three maximal paths: A→B→C→D→E, A→B→D→E→C, and A→B→E→C→D. Note that C, D, and E are represented more than once in the dominance tree because of their nonhierarchical relationships. The maximal subset (in this example, formed by C, D, and E) in which each member reaches all the others is called a "strong component" in graph theory. If each strong component is considered as a unit, and, given two units X and Y, [X,Y] = 1 if there exist a member x of X and a member y of Y such that $[x,y] = 1$, then the graph formed by these units and their relationships is called a reduced graph of the structure. Thus, the dominance tree of the example above can be represented by the diagram A→B→{C,D,E}, in which the keys enclose the members of the maximum strong component. Under the assumption of transitivity, every reduced graph of a dominance structure is a hierarchy, so we can analyze the reduced graph of a nonhierarchical structure with the concepts used here.

Reduced graphs are also useful for describing situations in which two or more lineages merge, as in A→B→C→D→F→G, A→B→E→F→G (see Dominance Tree Analysis of Empirical Data below).

Algorithm for Constructing Dominance Trees

In this work we constructed dominance trees with the use of DOMINA, a Delphi application that can be sent upon request. The general features of the algorithm are described below.

Initialization

A. Construct the dominance matrix, with one if the row member won the column member, or zero otherwise.

B. To find the transitive closure of the dominance matrix, impose transitivity to the matrix by the repeated application of the assumption of transitivity until the matrix does not change any more. The resultant matrix is the transitive matrix of dominance.

C. Select a given member R as the root of the tree representation.

Steps

1. Enumerate all the paths from R to the other members.
2. Discard the non-maximal paths.
3. Discard the redundant paths (i.e., paths whose information is already present in another path).
4. Stop.

The result of the algorithm is a set of paths that can be represented as a hierarchical tree rooted at R. Every path of the tree is elementary (a member of the path is traversed only once), but a member may be represented in more than one lineage in the tree.

DOMINA also produces a text file containing the transitive matrix, the dominance tree, and the tree-dominance matrix of each member; a list of the ties of the dominance matrix; the partial-dominant and partial-subordinate sets; and the strong components of the transitive matrix.

Dominance Tree Analysis of Artificial Data

To illustrate the properties and some of the potential applications of dominance trees for describing dominance structures, we applied this method to a hypothetical data set that was constructed to mimic complex social interactions, expressed as violations of the hierarchical properties (irreflexivity, asymmetry, and transitivity), that may occur in empirical dominance matrices.

The seven artificial dominance data sets are shown in Table I, row *a*. Dominance matrix 1*a* is a linear hierarchy, and dominance matrices 2*a* and 3*a* are partial hierarchies. The dominance matrices 4*a* and 5*a* are not hierarchical, but they become hierarchical under the assumption of transitivity: transitive matrix 4*a* is a linear hierarchy, and transitive matrix 5*a* is a partial hierarchy. In relation to data sets 6 and 7, neither the dominance nor the transitive matrices are hierarchical. The tree dominance analysis of the seven data sets gives the following results:

Dominance matrix 1*a* is a typical linear hierarchy (index of linearity equal to 1.000) in which the member A dominates the other members, B dominates the other members except A, C dominates the other members except A and B, etc. Note that when the transitive matrix is identical to the dominance matrix, no information is added by the assumption of transitivity. The dominance tree of each of the five members is represented in Fig. 1a–e. The relative hierarchical position of a given member can be measured by the number of individuals it dominates in its dominance tree (see matrix 1*a*). The complete representation of the structure is given by the dominance tree of the dominant member A (Fig. 1a), in which each member is ranked according to its hierarchical position. It strictly provides all the information of the dominance matrix, as can be seen by the tree-dominance matrix of member A, matrix 1*b*. Notice that the dominance trees of the other members are merely subpaths in the dominance tree of member A. Member E is the subordinate member of the structure.

TABLE I. Dominance Tree Analysis of Seven Hypothetical Dominance Date

1						
a	A	B	C	D	E	
A		1	1	1	1	4
B			1	1	1	3
C				1	1	2
D					1	1
E					1	0
	0	1	2	3	4	
b	A	B	C	D	E	
A		1	1	1	1	*
B			1	1	1	
C				1	1	
D					1	
E						

2						
a	A	B	C	D	E	
A		1	1	1	1	4
B						0
C						0
D						0
E						0
	0	1	1	1	1	
b	A	B	C	D	E	
A		1	1	1	1	*
B						
C						
D						
E						

3						
a	A	B	C	D	E	
A		1	1	1	1	4
B				1		1
C					1	1
D						0
E						0
	0	1	1	2	2	
b	A	B	C	D	E	
A		1	1	1	1	*
B				1		
C					1	
D						
E						

4						
a	A	B	C	D	E	
A		1	+1	+1	+1	4
B			1	+1	+1	1
C				1	+1	1
D					1	0
E						0
	0	1	2	3	4	
b	A	B	C	D	E	
A		1	1	1	1	*
B			1	1	1	
C				1	1	
D					1	
E						

5						
a	A	B	C	D	E	
A		1	+1			4
B			1			3
C						2
D					1	1
E						0
	0	1	2	0	1	
b	A	B	C	D	E	
A		1	1			*
B			1			
C						
D					1	*
E						

6						
a	A	B	C	D	E	
A		1	1	1	1	4
B			1	1	1	3
C			=1	1	+1	2
D		+1	=1	1		2
E			1	+1	=1	2
	0	1	4	4	4	
b	A	B	C	D	E	
A		1	1	1	1	*
B			1	1	1	
C			1	1	1	
D			1	1	1	
E			1	1	1	

7						
a	A	B	C	D	E	
A	=1	1	1	1	+1	4
B	+1	=1	1	1	1	4
C	+1	+1	=1	1	1	4
D	+1	+1	+1	=1	1	4
E	1	+1	+1	+1	=1	4
	4	4	4	4	4	
b	A	B	C	D	E	
A	1	1	1	1	1	*
B	1	1	1	1	1	*
C	1	1	1	1	1	*
D	1	1	1	1	1	*
E	1	1	1	1	1	*

1) Members are labelled from A to E; 2) zero values are omitted; 3) major row *a*: dominance (unsigned 1-valued cells) and transitive (unsigned 1-valued cells plus signed 1-valued cells added by the assumption of transitivity: '=', diagonal cells; '+', off-diagonal cells) matrices; italized numbers in column six of each matrix: number of members reached by the respective row member in its dominance tree; italized numbers in row six of each matrix: number of members that reach the respective column member in its dominance tree; 4) major row *b*: tree-dominance matrix of the row(s) member(s) marked by asterisk.

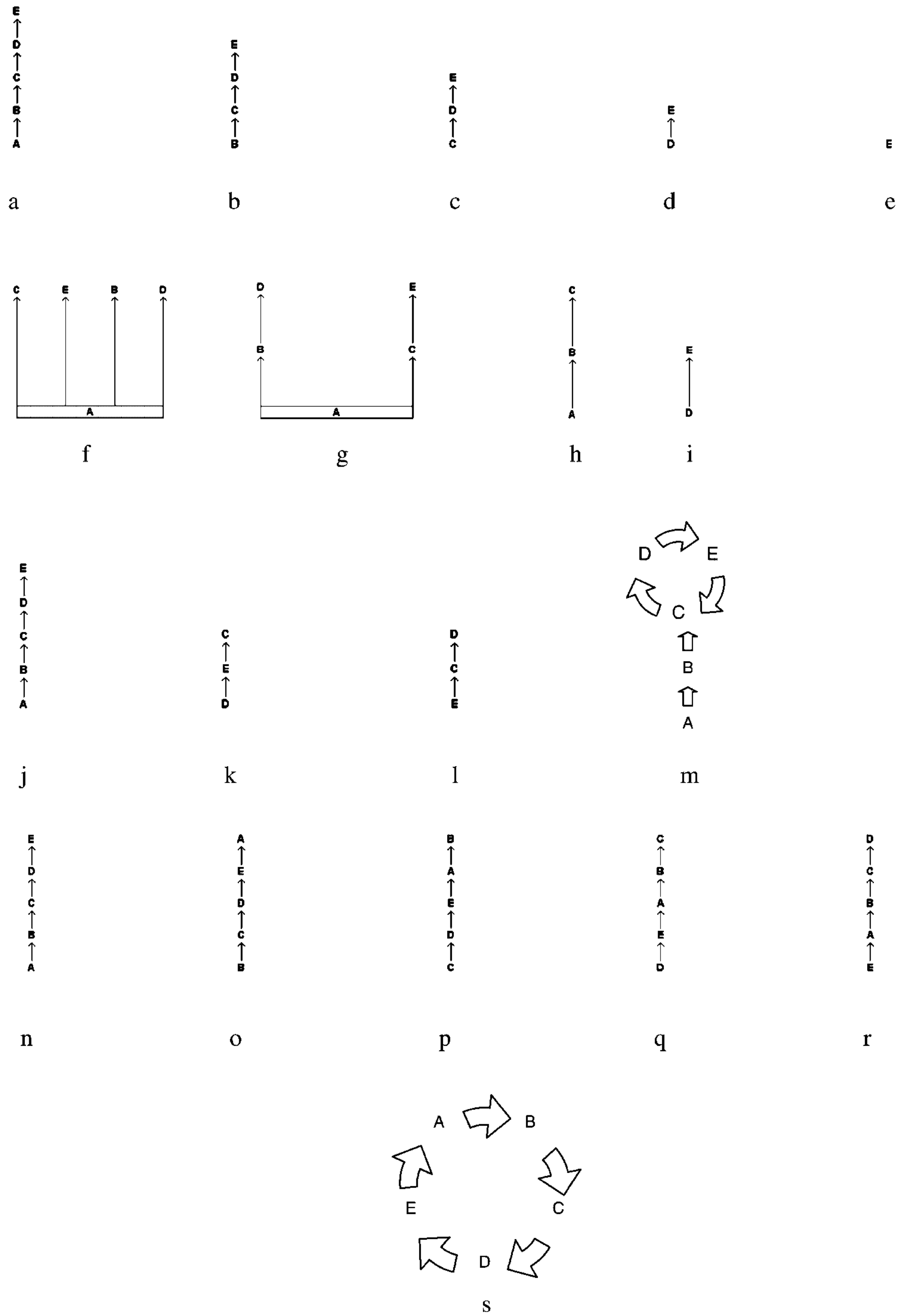

Fig. 1. Dominance trees of the artificial data in Table I: (**a–e**) data 1, (**f**) data 2, (**g**) data 3, (**h** and **i**) data 5, (**j–m**) data 6, and (**n–s**) data 7.

Dominance matrix 2*a* is a particular type of partial hierarchy, the despotic structure, in which the dominant member A dominates other members and no dominance relationship exists among the other members (i.e., all members, except A, are partial-subordinate members). As occurs for every hierarchical structure, the transitive matrix is identical to the dominance matrix. Figure 1f illustrates the tree diagram of member A that completely represents the structure. The tree-dominance matrix of A is identical to the dominance matrix. The dominance trees of the other members (not represented here) contain only one member (the root).

Dominance matrix 3*a* is a partial hierarchy with two lineages—A→C→E and A→B→D—emerging from the dominant member A, with D and E being the two partial-subordinate members. Again, notice that the dominance and transitive matrices are identical. The most informative tree is that of the dominant member A (Fig. 1g). The tree-dominance matrix of A is identical to the dominance matrix.

Dominance matrix 4*a* is not hierarchical because it fails to be transitive. However, after the dominance-directed tree analysis is applied, the resulting transitive matrix is a linear hierarchy that is identical to the dominance matrix 1*a*. The dominance trees of matrix 4*a* (not represented here) are identical to that represented in Fig. 1a–e. The assumption of transitivity allows us to imply linear hierarchy where only the adjacent members of the lineage show dominance relationships. The tree representation of member A recovers all the information of the transitive matrix (its tree-dominance matrix is identical to the transitive matrix).

In the dominance matrix 5*a* there are two independent substructures. An inspection of the dominance trees allows us to detect two independent lineages: A→B→C and D→E. To represent the dominance structure, we need the trees of the two partial-dominant members A and D (Fig. 1, trees h and i). Thus, to retrieve all the information of the transitive matrix we need to sum up the tree-dominance matrices of member A and D (the resultant matrix is the tree-dominance matrix 5*b*).

In the transitive matrices of examples 4 and 5, the assumption of transitivity affects only off-diagonal cells, that is, no circular triads are introduced. The following analysis of data 6 and 7 are examples of a more severe type of distortion.

The dominance matrix 6*a* represents a dominance structure that mixes hierarchical and nonhierarchical properties: on the one hand are dominant members A (which dominates all other members) and B (which dominates all other members except A), and on the other hand are circular triads involving C, D, and E. Note that the diagonal entries of the transitive matrix 6*a* for C, D, and E do not obey the irreflexivity property. The dominance tree that recovers most information from the transitive matrix is that of member A (Fig. 1j). This tree-dominance matrix is identical to the transitive matrix. However, the trees of members D and E show the circularity (Fig. 1k–l) and a reduced graph represents the circularity (Fig. 1m).

Finally, dominance matrix 7*a* is obtained by two modifications of dominance matrix 1*a*, with the cell [A,E] becoming zero and the cell [E,A] becoming one. The matrix is by no means hierarchical and the assumption of transitivity maximally distorts the dominance matrix, as can be seen by the reflexivity of the transitive matrix (in the transitive matrix 7*a*, all diagonal cells are one-valued). Although there are some differences in the tree representation of each member (see Fig. 1n–r), which may be explored if a deeper investigation of the dominance relationships is needed, the basic dominance information is that each member dominates all the other members. To retrieve the dominance information from the matrix, all the dominance trees must be inspected. In fact, the transitive matrix can be retrieved only by summing up the tree-dominance matrices of all five members (matrix 7*b*). A reduced graph represents the circularity (Fig. 1s).

Evaluation of Distortion

The distortion produced by the assumption of transitivity may be measured by the amount of intrusive information added to the dominance matrix. If the dominance matrix is a hierarchical structure, then the transitive matrix is equal to the dominance matrix and the distortion is zero (see the matrices for data 1–3 in Table I).

A mild degree of distortion occurs when the assumption of transitivity does not produce information that contradicts the irreflexivity property, as indicated in data sets 4 and 5 in Table I. Every method of data simplification may imply some distortion of the original data. To evaluate the pros and cons of a given method, we need to balance the degree of distortion produced by it, and its ability to uncover the ‘‘subjacent’’ structure of the data. An analysis of matrix 4*a* is illustrative in this respect.

The transitive matrix 4*a* shows a lot of new dominance information. Its transitive matrix is equal to the linear (complete) hierarchical dominance matrix 1*a*. Given the assumption of transitivity, the four dominance relationships of matrix 4*a* are sufficient to produce a linear hierarchy, and in this respect are more parsimonious than matrix 1*a*. In some sense, matrix 1*a* has redundant dominance information that we can completely retrieve by applying the assumption of transitivity on a more parsimonious dominance matrix (matrix 4*a*).

The great degree of distortion occurs when the dominance matrix has circular triads, as in matrix 6*a* and, particularly, matrix 7*a*. The corresponding transitive matrices show diagonal cells in which the property of irreflexivity is disobeyed. Despite the great amount of distortion introduced by the assumption of transitivity, the dominance tree analysis may be still useful for describing the structure, as can be seen in Fig. 1j. In this figure the mixed structure of matrix 6*a* may be represented by the tree structure $A \rightarrow B \rightarrow \{C,D,E\}$, where the members in brackets form a subset in which every member reaches the others. In the transitive matrix 7*a*, every member reaches all the other members. Therefore, all members form the unique strong component {A,B,C,D,E}. In this case, the dominance structure cannot be fully represented by any single dominance tree.

Information Conveyed by a Dominance Tree Analysis

The dominance tree allows a flexible evaluation of the role and status of each member in the structure to be performed. Particularly for the linear hierarchy, the dominant member is that which reaches all the others but is not reached by anyone, and the subordinate member is that which does not reach anyone but is reached by all others. Given that a given hierarchy may be partial or may be formed by two or more independent subsets of members, we have to enumerate the members that are in the partial-dominant or partial-subordinate set (for example, in a partial hierarchy with two lineages there are two members in the subordinate set, one for each lineage). Then, the partial-dominants are members of the set of individuals that are not reached by anyone, whereas the partial-subordinates are members of the set of individuals that do not reach anyone. The isolated members are simultaneously partial-dominant and partial-subordinate.

They are easily enumerated by finding the intersection (in set theory terms) of the partial-dominant and partial-subordinate sets.

In practice, only the dominance trees of the partial-dominant members are relevant to an analysis of the structure. Other members produce trees with redundant information. The information of the transitive matrix is retrieved only by summing up the tree-dominance matrix of each partial-dominant member.

A rank may be constructed by attaching, for each member, the number of individuals it reaches in its dominance tree (see the numbers in column 6 of each matrix of row *a*, Table I). In the linear hierarchies of matrices 1*a* and 4*a* (Table I) these numbers have a simple meaning in terms of the hierarchical rank of the individuals. In the partial hierarchies of matrices 3*a* and 5*a* (Table I) these numbers are only meaningful in terms of the hierarchical rank of the individuals in each lineage—they are meaningless for different lineages. Thus, in matrix 5*a*, rank 2 for B is not directly comparable to rank 2 for E because they pertain to different lineages (see that B is not a subordinate member, whereas E is).

Dominance Tree Analysis of Empirical Data

To illustrate the practical usefulness of the dominance tree analysis, we applied the method to infer the dominance structure of a semifree-ranging group of brown capuchin monkeys (*Cebus apella*). These data were collected by R.G.F. from a group of 17 individuals (three adult males, two subadult males, four adult females, and eight immatures of both sexes) inhabiting a peninsula of 18 ha within the Tietê Ecological Park (São Paulo, Brazil), a reforested area where the animals were introduced (for further details on the study group and site, see Ottoni and Mannu [2001] and Ferreira et al. [2002]). The indicators of dominance used in this work included aggression/receive aggression (chase, bite, or aggressive display), approach/retreat, and displace/be displaced. Data were collected on an all-occurrences basis. Only clear dyadic interactions were used. The data used here comprise ca. 500 hr of observations collected from February 2000 to January 2001 [Ferreira, 2003].

The dominance matrix of the studied group (Table II) is not hierarchical because it fails to be transitive. Zero ties accounted for 46 dyadic relations. Three dyads had low-value above zero ties, all between immature males (EdMj $\times$ MnMj = 1; FrMj $\times$ LbMj = 1; MnMj $\times$ DwMi = 1). After the dominance-directed tree analysis is applied, the resulting transitive matrix (Table III) is a partial hierarchy with several lineages emerging from the partial-dominant partial-subordinate members. The treatment of ties and imposition of transitivity introduced 27 dominance relations to the matrix, but did not provoke severe distortions in the original structure. In particular, no information was added to the main diagonal (i.e., the irreflexivity was not violated by the assumption of transitivity).

The most informative tree is that of the dominant member BqMa (Fig. 2). The tree-dominance matrix of BqMa is identical to the dominance matrix. Several paths are represented more than once in the dominance tree due to their nonhierarchical relationships. Thus, the dominance tree can be represented by the reduced graph of Bq's dominance tree (Fig. 3), in which the individuals are ranked by the number of vertices presented on their trees. The reduced graph shows the adult male Bq as the dominant member, followed by the adult female Me. Three adults emerge with different ranks (AnFa and SuMa: rank 3; FiFa: rank 7). Then a merging occurs, with members AnFa and SuMa dominating the member MeMa (rank 4). The structure splits again into different lineages

TABLE II. Dominance Matrix of Empirical Data From a Semifree Group of *Cebus apella*

	BqMa	SuMa	MeMa	ElMs	PeMs	EdMj	FrMj	VsFj	LbMj	CsFj	MnMj	QuMi	DwMi	FiFa	AnFa	MeFa	JaFa
BqMa		3	4	6	6	8	4	5	5	2	10	15	1	1	5	4	8
SuMa			3	0	2	0	2	0	1	0	0	0	0	0	0	0	0
MeMa	0	1		3	5	2	4	4	3	0	2	1	0	0	0	0	2
ElMs	0	0	0		12	10	14	9	8	5	9	7	2	0	0	0	1
PeMs	0	0	0	0		0	0	1	1	6	0	0	1	0	0	0	0
EdMj	0	0	0	0	0		0	22	4	2	1	3	3	0	0	0	0
FrMj	0	0	0	0	0	0		0	1	6	0	0	0	0	0	0	0
VsFj	0	0	0	0	0	0	0		0	3	0	1	0	0	0	0	0
LbMj	0	0	0	0	0	0	1	1		4	0	2	1	0	0	0	0
CsFj	0	0	0	0	0	0	0	0	0		0	0	0	0	0	0	0
MnMj	0	0	0	0	0	1	0	4	1	2		1	1	0	0	0	0
QuMi	0	0	0	0	0	0	0	0	0	0	0		0	0	0	0	0
DwMi	0	0	0	0	0	0	0	0	0	3	1	0		0	0	0	0
FiFa	0	0	0	0	0	0	2	3	0	0	1	1	0		0	0	0
AnFa	0	0	1	0	0	2	0	1	0	0	2	1	0	0		0	0
MeFa	0	1	2	0	1	0	0	2	1	0	1	2	2	2	3		2
JaFa	0	0	0	0	1	0	2	2	1	2	2	0	5	0	0	0	

M, male; F, female, a, adult; s, subadult; j, juvenile; i, infant.

TABLE III. Dominance ("Unsigned 1×0") and Transitive ("Signed 1×0") Matrix (Zero Values Omitted) of empirical Data From a Semifree Group of *Cebus apella*

	BqMa	SuMa	MeMa	ElMs	PeMs	EdMj	FrMj	VsFj	LbMj	CsFj	MnMj	QuMi	DwMi	FiFa	AnFa	MeFa	JaFa
BqMa		1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
SuMa			1	+1	1	+1	1	+1	1	+1	+1	+1	+1				+1
MeMa		1		1	1	1	1	1	1	+1	1	1	+1				1
ElMs					1	1	1	1	1	1	1	1	1				1
PeMs								1	1	1		+1	1				
EdMj								1	1	1		1	1				
FrMj										1							
VsFj										1		1					
LbMj								1		1		1	1				
CsFj																	
MnMj						1		1	1	1		1	+1				
QuMi																	
DwMi										1							
FiFa							1	1	+1	+1	1	1	+1				
AnFa			1	+1	+1	1	+1	1	+1	+1	1	1	+1				+1
MeFa		1	1	+1	1	+1	+1	1	1	+1	1	1	1	1	1		1
JaFa					1		1	1	1	1	1	+1	1				

M, male; F, female, a, adult; s, subadult; j, juvenile; i, infant.

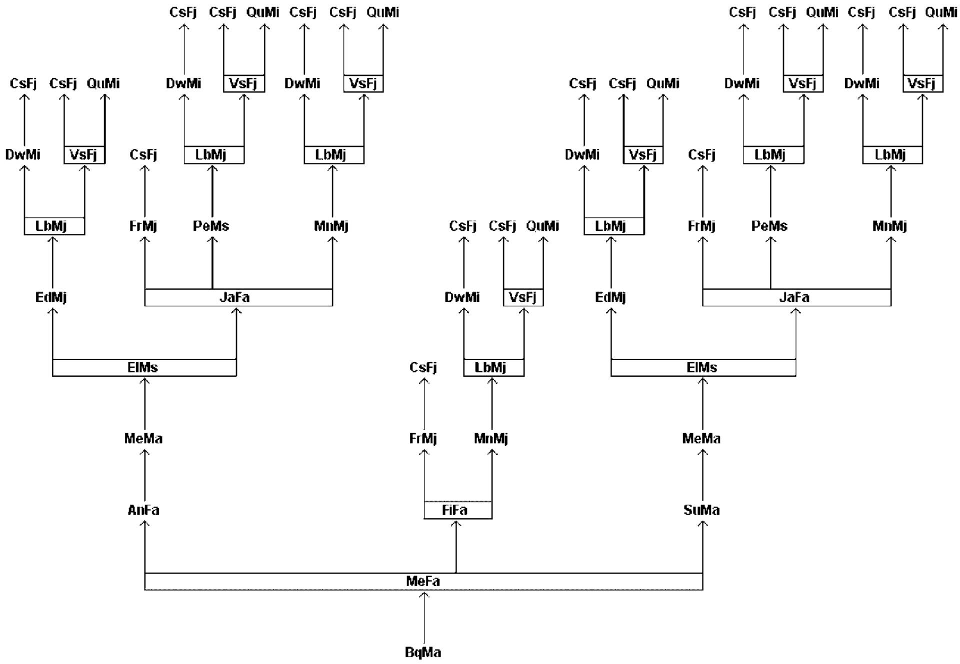

Fig. 2. Dominance tree of the dominant member based on empirical data from a semifree group of capuchin monkeys (Tables II and III). M = male, F = female, a = adult, s = subadult, j = juvenile, i = infant.

from ranks 5, 6, 8 and 10, but these lineages are merged through common subordinate members at ranks 8 (FiFa and JaFa dominating MnMj), 9 (three lineages dominating LbMj), 11 (FiFa and JaFa dominating FrMj), and 12 (three lineages dominating CsFj). In each case, the common subordinate member is a juvenile.

The resulting partial-dominance hierarchy, with more than one individual occupying the same rank position, is related to the absence of actual aggressive conflicts between some members. The absence of aggressive conflicts can be credited to an avoidance strategy adopted by subordinate group members [Izar & Sato, 1997] or to tolerance from dominant members [Izar, 2004]. In fact, according to socioecological models, tolerant dominance hierarchies are expected when primate groups are subjected to strong food competition within and between groups [Sterck et al., 1997]. This kind of structure cannot be properly assessed by other methods, as stated in the Introduction.

CONCLUSIONS

In this work we defined a social structure by its set of members and set of dominance relationships. A hierarchy is a structure that must be irreflexive, asymmetric, and transitive. If all pairs of members show dominance relationships, the hierarchy is said to be linear; otherwise, it is a partial hierarchy. Structures may mix hierarchical and nonhierarchical properties, or they may be nonhierarchical.

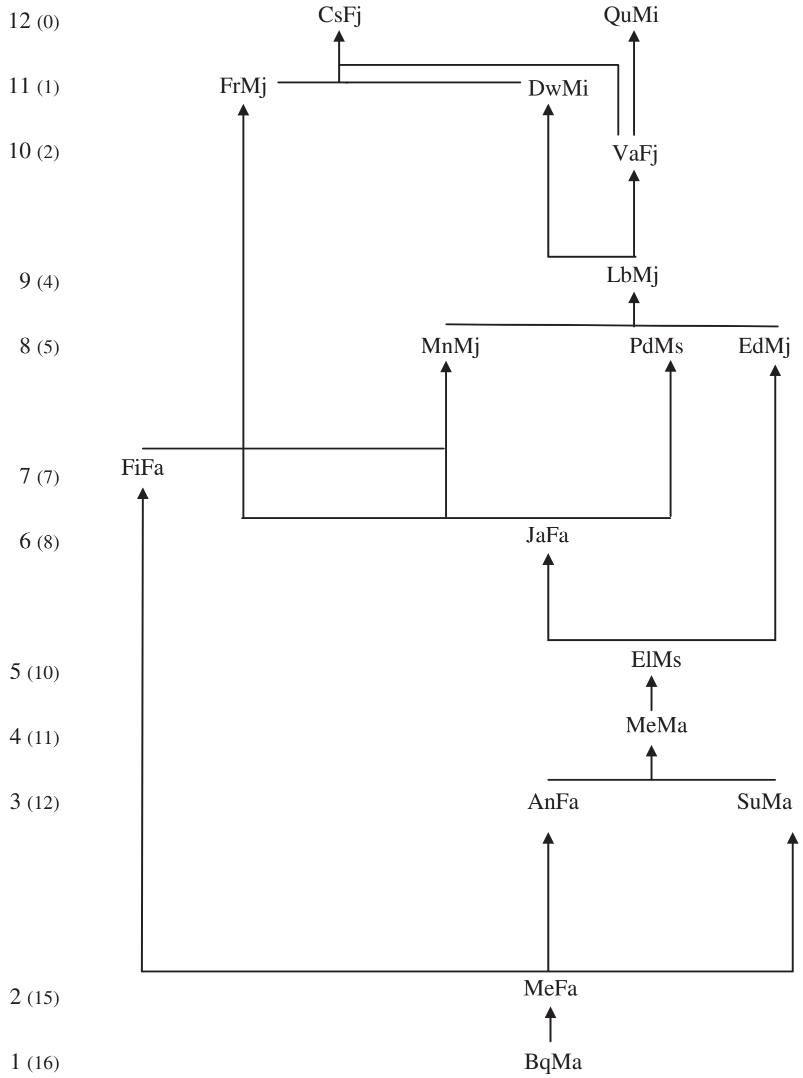

Fig. 3. Reduced graph from the dominance tree of the dominant member in a semifree group of capuchin monkeys. M = male, F = female, a = adult, s = subadult, j = juvenile, i = infant. The figures to the left indicate the rank based on the number of individuals dominated (shown in brackets).

Current methods for describing dominance relationships are devised to only distinguish linear from nonlinear structures. Nonlinear structures may or may not be hierarchical, but an index of linearity is not able to make this distinction. In particular, the index cannot detect partial hierarchies.

Dominance tree analysis is proposed to distinguish these diverse forms of organization. By abandoning the approach of encompassing all descriptions of the structure in only one index, or trying to force all members into a ranked list of individuals, dominance tree analysis demands more involvement on the part of the analyst to interpret the results (i.e., the analysis of all dominance trees, evaluation of the status of each member in the tree structure, occurrence of circular triads, etc.). In so doing, dominance tree analysis allows the researcher to perform a richer and more flexible analysis of the organization of the dominance relationships than the current methods. A distinctive feature of dominance tree analysis is that it is devised not only to detect hierarchical organizations, but also to determine when hierarchical and nonhierarchical principles are operating in different subsets of individuals. In so doing, it provides a simple tree representation where both situations are clearly differentiated.

The degree of distortion produced by the assumption of transitivity may be explicitly evaluated by inspecting the amount and the nature of the extra dominance relationships introduced by the assumptions of the dominance matrix. Departures from the hierarchical principles can be measured by the amount of violations of the principle of irreflexivity. These violations of irreflexivity may be generalized or may be restricted to some cells. Dominance tree analysis is able to distinguish between these mixed cases, with hierarchical and nonhierarchical principles operating in different places of the structure.

Each member may be the root of the dominant tree. So, from a structure with N members, a total of N trees may be constructed, but only those of the partial dominant members are relevant for describing the structure. The other trees can be discarded because they show redundant information. The analysis of the dominant trees allows us to describe the characteristics of the dominant structure, whether it is hierarchical or not, as well as the hierarchical status of each member in the structure. The degree of importance of a given member may be evaluated by the number of individuals it dominates in its dominance tree, and thus a rank may be constructed even if some dyads fail to show hierarchical relationships. The number of relevant dominance trees is directly related to the complexity of the structure. For example, any linear hierarchy requires only the dominance tree of the dominant member. This tree encompasses all of the information from the dominance matrix or the tree dominance matrix. At the other extremes, all dominance trees are needed to describe the structure in which any member is involved in circular triads with any other two members (that is, in which the tree dominance matrix is reflexive).

Dominance trees allow the identification of different substructures in a partial hierarchy. These substructures may take the form of different lineages beginning from a common substructure, or that of independent substructures, or they may even constitute a subset of members in which no hierarchical relationships occur.

The use of dominance trees to describe dominance structures relies on the validity of adopting the assumption of transitivity. When the structure is already hierarchical, irrespectively of being linear or partial, the assumption of transitivity does not produce any change in the dominance matrix. Minor distortions resulting from the introduction of dominance relationships into the off-diagonal cells may appear, but they do not constitute a real impediment to uncovering the hierarchical nature of the dominance relationships in the group.

Important distortions occur when the assumption of transitivity introduces reflexivity into the transitive matrix. In that case the entire structure is not strictly hierarchical; however, dominance tree analysis is still able to show where the hierarchical property of irreflexivity is obeyed and where it is not obeyed. Thus it can provide a detailed description of the mixed dominance structure (e.g., where hierarchy occurs, which members are involved in nonhierarchical circular triads, the status of each member, etc.).

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