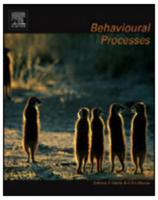
Behavioural Processes 88 (2011) 168–176

Contents lists available at SciVerse ScienceDirect

Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc



Effect of unknown relationships on linearity, steepness and rank ordering of dominance hierarchies: Simulation studies based on data from wild monkeys

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ARTICLE INFO

Article history:
Received 5 February 2011
Received in revised form 9 July 2011
Accepted 9 September 2011

Keywords:
Dominance hierarchy
Linearity
Rank order
Steepness
Unknown relationships

ABSTRACT

The presence of unknown dyadic relationships is a common problem in constructing dominance hierarchies for groups of social animals. Although previously acknowledged, the influence of unknown relationships on hierarchy measures like linearity and steepness has not been studied in detail. Using real data-sets from four groups of wild monkeys, we illustrate how unknown relationships affect linearity and steepness of hierarchies and the consistency of rank ordering based on de Vries' I&SI method. Monte Carlo simulations revealed significant negative linear relationships between the proportion of unknown relationships and both linearity and steepness. These simulations over-estimated steepness and linearity indices relative to additional real-data input matrices. Rank orders became inconsistent at 26–38% unknown relationships, depending on the group. Group size and the specific input matrix substantially affected how much unknown relationships influenced steepness and linearity, the values of these indices and the point at which rank order became inconsistent. We recommend caution in characterizing the dominance structure of a group with many unknown relationships, and in drawing conclusions about hierarchy linearity and steepness based on few input matrices, especially if they contain many unknown relationships. Quantitative characterizations of hierarchies are perhaps best viewed as a somewhat fluid range rather than fixed values.

1. Introduction

Dominance status is an important social variable that influences individual behavior and life history in group-living animals (Drews, 1993; Whitehead, 2008). Many researchers examine correlations between dominance and fitness-related measures, like reproductive success (e.g., Ang and Manica, 2010; Muniz et al., 2010; Vervaecke et al., 2007) and susceptibility to disease (Sapolsky, 2005). Characterizing aspects of the hierarchy as a whole, such as its linearity, steepness, stability or the typical asymmetry of the underlying pairwise relationships (directional consistency, Van Hooff and Wensing, 1987) may also contribute to comparative analyses of animal social systems (de Vries et al., 2006; Isbell and Young, 2002; Langbein and Puppe, 2004).

Researchers examining the determinants and effects of dominance status use quantitative methods to rank individuals based on patterns in observed behavior. A first step in constructing dominance hierarchies is deciding what kinds of social interactions (usually, asymmetrical contest-related behavior) to include in the analysis (Drews, 1993; Whitehead, 2008). A second decision concerns how the social interaction records are used to construct a hierarchy. Methods for computing dominance hierarchies emphasize different aspects of agonistic behavior and outcomes of dyadic encounters, and each is based on particular assumptions. Choosing which method to apply in a given situation may be difficult (Bang et al., 2010; Bayly et al., 2006; de Vries and Appleby, 2000; Gammell et al., 2003; Hemelrijk et al., 2005; Whitehead, 2008). Such a choice is critical, however, as even ordinal rankings may vary depending on the method (Bayly et al., 2006; Hemelrijk et al., 2005; Whitehead, 2008), and different methods vary in their response to peculiarities of the input data (Bayly et al., 2006; de Vries, 1998; de Vries and Appleby, 2000; Gammell et al., 2003; Hemelrijk et al., 2005).

A common problem in real datasets is the presence of unknown relationships. Two individuals have an unknown relationship when there are no records of behavioral interaction relevant to deducing their relative dominance status. An absence of records may reflect a real lack of interactions or sampling limitations. The presence of unknown relationships decreases the calculated linearity of a hierarchy (Archie et al., 2006; Galimberti et al., 2003; Isbell and Young, 2002; Koenig and Borries, 2006; Lu et al., 2008; Robbins et al., 2005; Vogel, 2005) and can affect the statistical significance of the linearity index (Appleby, 1983; de Vries, 1995; Koenig and Borries, 2006). Some methods have been specifically designed to accommodate the presence of unknown relationships (de Vries, 1995, 1998; Jameson et al., 1999; Singh et al., 2003; Wittemyer

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doi:10.1016/j.beproc.2011.09.003

and Getz, 2006). For example, de Vries (1995), in developing a test of the statistical significance of a hierarchy's linearity using the I&SI (Inconsistencies and Strength of Inconsistencies) method, defined a modified linearity index (h') that aims to correct for unknown and tied relationships and is now widely used.

The index of hierarchy steepness as derived from the David's score cardinal ranking method (David, 1987; de Vries et al., 2006; Gammell et al., 2003) is relatively new (de Vries et al., 2006; Flack and de Waal, 2004) and as such the potential effects of unknown relationships on steepness have so far received little attention (but see Bang et al., 2010 for the effect of unknown relationships on the uniqueness of David's scores in artificial data). In addition, while a negative linear correlation between the percentage of unknown relationships and linearity has been established (Galimberti et al., 2003; Robbins et al., 2005), this negative relationship has not been studied in detail.

Unknown relationships also increase the probability that a hierarchy analysis will produce multiple equally linear rank orders. The I&SI method and other dominance indices have this problem (Bang et al., 2010; de Vries, 1998; de Vries and Appleby, 2000; Wittemyer and Getz, 2006), which seems typical of methods that aim to minimize inconsistencies within the hierarchy: individuals with few interactions (and thus few partners and many unknown dyadic dominance relationships) may have several equally plausible potential rank positions. Deciding between the various possible rank orders would be arbitrary (de Vries, 1998). The effect of unknown relationships on the consistency of the I&SI ranking has been acknowledged in methodological studies (de Vries, 1998; de Vries and Appleby, 2000), but when this method is applied to real data, this effect is rarely taken into account. To our knowledge the percentage of unknown relationships at which more than one equally linear rank order can be produced with the I&SI method has not been demonstrated empirically.

The effect of unknown relationships on several hierarchy characteristics, including the corrected index of linearity (h') and the steepness index derived from David's scores, became apparent to us when we analyzed dominance hierarchies as part of a long term study of social behavior of wild monkeys. We sought to apply methods and measures that are commonly used in studies of social animals (e.g., Chancellor and Isbell, 2009; Galimberti et al., 2003; Hewitt et al., 2009; Vervaecke et al., 2007), but found that unknown relationships in our sample affected the results. We therefore investigated explicitly the effect of unknown relationships on linearity and steepness indices, as well as the rank orderings produced by the I&SI method. We aimed to show how unknown relationships affect these hierarchy characteristics using several real data sets from multiple social groups of wild monkeys. To assess the effect of unknown relationships on linearity and steepness indices, we applied Monte Carlo simulation techniques to create reduced data sets with varying numbers of unknown relationships. We also compared our simulation results to the linearity and steepness indices derived from multiple additional real win–loss input matrices from our study groups.

2. Methods

2.1. Input data

We used dominance data from four groups (TWS, TWN, GN, GS) of blue monkeys (*Cercopithecus mitis stuhlmanni*) from a single population in the Kakamega Forest, Kenya. Each group had 16–49 members, including 6–20 adult females (recognized as such from the calendar year of their first offspring's birth date), their offspring excluding infants (up to one year old), and usually one adult male. In this species, females remain in their birth group for their entire lives, whereas males emigrate at puberty. Our analyses focused on the hierarchy among the groups' adult females only, as juveniles participate in relatively few agonistic interactions and appear to have dynamic ranks. The adult male invariably dominated all other individuals and was therefore also excluded.

We used data on agonistic interactions collected from 2000 to 2008. These interactions included supplant and avoid behavior as well as higher intensity aggression such as chasing and hitting. We included only dyadic interactions between identified individuals in which there was a clear winner and loser, such that one and only one individual showed submissive behavior (cower, flee, avoid, or was supplanted) or vocalizations (gecker, trill or scream).

We combined records of agonistic interactions from *ad libitum* and focal animal sampling to create win:loss input matrices for a given period: from 2000 to 2005 hierarchies were based on 12-month periods of *ad libitum* data only. From 2007 to 2008, data from focal animal samples were also available and we used the greater volume of data to construct dominance hierarchies for 6-month periods. For 2006, as focal sampling began in June, hierarchies were constructed for one 5-month period and one 7-month period. Each data matrix included 39–710 interactions (mean: 224).

2.2. Hierarchy measures

We used Matman 3.2 (Noldus Information Technology) to implement de Vries's (1998) I&SI method for evaluating linearity and for extracting a hierarchy from behavioral input matrices. This method minimizes the number and strength of inconsistencies within a reordered hierarchy. An inconsistency occurs when one individual ranks below another despite having won most of their agonistic interactions, and its "strength" is the rank difference between the two individuals in question (de Vries, 1998). Matman calculates de Vries's (1998) linearity index h' and produces a reordered matrix according to the above criteria. The linearity index varies from 1 (perfect linearity: every individual dominates all animals ranked below and none of those ranked above, with no circularities present in the hierarchy) to 0 (every individual dominates the same number of other individuals; de Vries, 1998). An associated p-value based on a sampling process using 10,000 randomizations assesses the statistical significance of the linearity index (de Vries, 1995). We also used Matman's output of the percentage of unknown relationships, which became the independent variable in our analyses.

In calculating the linearity index, Matman's I&SI method treats both unknown and tied relationships (opponents have equal numbers of wins/losses) as undecided (de Vries and Appleby, 2000) as both types of dyadic relationship have no clear winner or loser, but these are in fact two different types of dyad (de Vries, 1995). In Matman's linearity calculation, it is assumed that observers cannot know whether individual A would beat individual B or vice versa in an unknown relationship had they been observed to interact, and thus this relationship is assigned a value of 0.5 (equal probability of A being dominant to B and B being dominant to A) in matrix cells i,j and j,i. This is the same probability assigned to a relationship that is known to be tied (de Vries, 1995). Thus when determining degree of linearity with the I&SI method, using available observational data, both types of dyad are assigned the definition "undecided." However, it should be noted that while the I&SI ranking algorithm treats these separate cases identically, the presence of each contains very different information regarding the actual presence or absence of a clear dominance hierarchy within the social group. For example, if all relationships were observed to be tied, the linearity would equal zero and the hierarchy would be perfectly egalitarian (de Vries, 1995).

David's score (DS) is a cardinal ranking method in which rank differences express the magnitude of power differentials between