Animal Behaviour xxx (2018) 1–16

Contents lists available at ScienceDirect

Animal Behaviour

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

Forum Article

Dominance ranks, dominance ratings and linear hierarchies: a critique

Christof Neumann [a,*], David B. McDonald [b], Daizaburo Shizuka [c]

[a] Department of Comparative Cognition, University of Neuchâtel, Switzerland
[b] Department of Zoology & Physiology, University of Wyoming, Laramie, WY, U.S.A.
[c] School of Biological Sciences, University of Nebraska-Lincoln, NE, U.S.A.

ARTICLE INFO

Article history:
Received 5 October 2017
Initial acceptance 8 January 2018
Final acceptance 12 June 2018
Available online xxx
MS. number; 17-00792R

Keywords:
ADAGIO
David's score
dominance
dominance hierarchy
Elo-rating
I&SI
linearity
method validation
simulation
transitivity

Dominance is a core concept when studying the structure of animal societies. Dyadic dominance relationships in which one individual is dominant over another, subordinate, individual give rise to group level dominance hierarchies (Drews, 1993; Hinde, 1976). High rank in such hierarchies is often related to fitness-associated measures, for example high mating and reproductive success (e.g. Cowlishaw & Dunbar, 1991; Ellis, 1995; Rodriguez-Llanes, Verbeke, & Finlayson, 2009). As such, the assessment of dominance status and individual rank in a hierarchy is a crucial task, often done routinely, in animal behaviour studies.

Early methods of calculating dominance hierarchies focused mostly on the aspect of linearity, i.e. systems where one individual, A, dominates all other group members, while B dominates everyone but A, C dominates everyone but A and B, and so on. The major goal here was to recover from empirical dyadic interaction data an order of individuals that reflected this patterning (e.g. de Vries, 1998). More recently, researchers have recognized the additional importance of temporal variability of dominance status of individuals over time, the uncertainty associated with assigning rank metrics and the inclusion of prior knowledge to refine dominance assessment. This led to much progress in developing new methods and extending existing ones with respect to assessing dominance status (e.g. Adams, 2005; Fushing, McAssey, & McCowan, 2011; Izar, Ferreira, & Sato, 2006; Neumann et al., 2011; Newton-Fisher, 2017; Schmid & de Vries, 2013; Sánchez-Tójar, Schroeder, & Farine, 2018).

One of these recently introduced methods is ADAGIO (Douglas, Ngonga Ngomo, & Hohmann, 2017), which was expressly developed to handle data with insufficient linearity. Douglas et al. (2017; from here on: DNH) based the need for a new method on their finding that among published data sets strongly linear hierarchies are the exception, rather than the norm. The key feature of their new algorithm is that it allows deviations from a strictly linear order, i.e. several individuals can occupy the same ordinal rank. The ranking is achieved via directed acyclic graphs (DAGs), for which cyclic triads are stripped from the network during computation, i.e. triads in which individual A is dominant over B, B over C and C over A. To remove such a cycle, one edge (interaction(s) between either A and B, or B and C, or C and A) is removed from the network

* Correspondence: C. Neumann, University of Neuchâtel, Department of Comparative Cognition, Rue Emile Argand 11, 2000, Neuchâtel, Switzerland.
E-mail addresses: christofneumann1@gmail.com, christof.neumann@unine.ch (C. Neumann).

https://doi.org/10.1016/j.anbehav.2018.07.012

(transforming such triads into 'pass-along' triads, Shizuka & McDonald, 2012). Once such a cycle-free network is achieved, ordinal ranks can be assigned to all individuals, by either of two strategies (top-down or bottom-up), which allows the possibility in the final ranking that two or more individuals are assigned the same ordinal rank (Fig. 3 in DNH).

In this commentary, we wish to address a number of issues related to the introduction of ADAGIO, which in their combination lead us to be sceptical about the necessity for ADAGIO and, more importantly, its validity. First, we briefly revisit DNH's claim that most dominance data sets are not sufficiently linear to allow assigning a linear rank order. Second, we point out several problems with the validation approach employed by DNH to demonstrate ADAGIO's superiority over alternative methods. Third, we address some of the advantages other methods have over ADAGIO. Finally, we investigate the question of how the choice of method to assign dominance matters in practical terms.

MOST DOMINANCE RELATIONS ARE TRANSITIVE

It is worth first clarifying the distinction between the concepts of linearity and transitivity in dominance hierarchies. The ADAGIO method is built on the concept of DAGs: i.e. dominance networks in which all triadic relations are transitive (i.e. not cycles). This concept of transitivity should not be equated with the concept of linearity as measured by the h' index (de Vries, 1995), as DNH have done. Perfect linearity ($h' = 1$) arises when all relations are observed and are transitive (Landau, 1951; see Appendix 1). Thus, it is possible to have DAGs that are not perfectly linear, when there are dyads in the group for which the dominant–subordinate relation is unknown. The general pattern of decrease in h' with increasing proportion of unknown dyads has been well documented (Fig. 1a; de Vries, Netto, & Hanegraaf, 1993; de Vries, 1995; Klass & Cords, 2011; Norscia & Palagi, 2015; Shizuka & McDonald, 2012, 2015). Using a metric that is much less sensitive to sparseness (triangle transitivity, P_t, Fig. 1b), two of us showed that transitivity is overwhelmingly common (Shizuka & McDonald, 2012, 2015). Thus, the reason the majority of published dominance data sets do not exhibit 'strong linearity' ($h' \geq 0.9$, DNH's criterion, Appendix 1) is not the lack of transitivity; it is simply that most dominance networks contain considerable proportions of unknown relationships, especially in larger groups (Appendix Fig. A1; Shizuka & McDonald, 2012).

We agree with DNH that there is much room for conceptual advances in understanding hierarchical structures that are not strictly transitive. Data sets with at least one cyclic triad do occur and resolving dominance rankings in these cases continues to be an important consideration. However, DNH overstate the problem regarding the lack of linearity in animal dominance data by using an inappropriate benchmark that is arbitrary and subject to bias (Appendix 1; see also de Vries et al. (1993), Whitehead (2008), and Farine (2017) for more general discussions of the use of appropriate null models in network analysis). The preponderance of evidence suggests that the majority of empirical dominance networks mostly consist of transitive dominance relations, and that attempting to find linear orders is justified and worthwhile more often than not.

PROBLEMS WITH DNH'S VALIDATION OF ADAGIO

One of the major goals of DNH was to assess the performance of ADAGIO by comparing the ranks produced with ADAGIO to the results of other popular ranking methods: I&SI (Schmid & de Vries, 2013; de Vries, 1998), David's score (David, 1987; Gammell, de Vries, Jennings, Carlin, & Hayden, 2003) and Elo-rating (Albers & de Vries, 2001; Elo, 1978). Results of this approach indicated that ADAGIO, across a number of different scenarios, came on average closer to benchmark ranks, by between about 0 and 1 ranks (Fig. 5 in DNH). Here, we point out several methodological flaws in this validation approach that lead us to be sceptical about the results of DNH.

In their simulations, DNH generated data sets of dyadic dominance interactions. The outcomes of these interactions were probabilistically determined by predefined ranks of all individuals ('true' ranks), i.e. in a dyadic interaction the individual with higher true rank was more likely to win this interaction than the individual with lower true rank. DNH then used the average Euclidean distance between 'true' ranks of all individuals and the ranks recovered by the different methods to quantify the performance of the different ranking algorithms relative to each other. This approach is one valid way to measure the difference between 'true' assigned ranks and the measured ranks/scores, but sole reliance on Euclidean distances can generate misleading conclusions. Take, for example, cases in which there are ties in the true ranks, such as 1, 2, 3, 3, 3. Here, the number of unique ranks is smaller than the number of individuals (3 versus 5). Methods that can reproduce this ranking are ones that accommodate tied ranks/identical scores

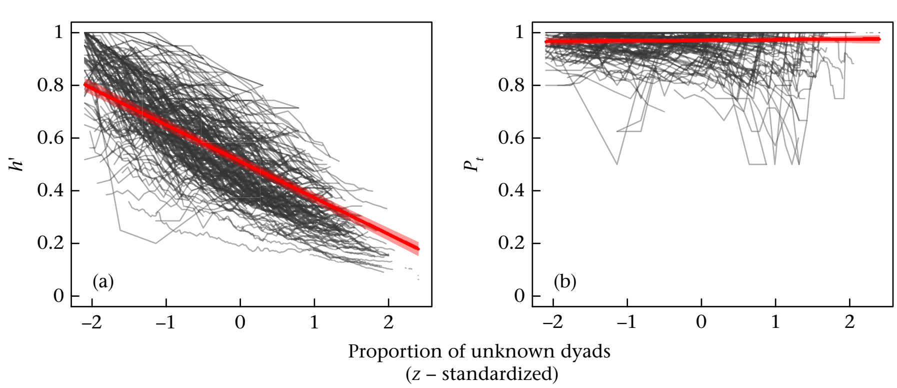

Figure 1. Removal experiment on 256 empirical data sets. The figure shows the relationships between network sparseness (proportion of unknown dyads) and (a) the linearity index h' and (b) triangle transitivity P_t. Starting from the original dominance matrix, we randomly removed one interaction and recalculated all indices. If, for a given data set and value of sparseness, more than one possibility existed (matrices with the same sparseness but different total weight), we chose one randomly. Red lines are fitted lines from a regression model with sparseness as fixed predictor variable and matrix ID as random intercept (with random slope for sparseness). Data were taken from Shizuka and McDonald (2015) and Douglas et al. (2017), and only groups with at least four individuals were included. (For interpretation of the references to color/colour in this figure legend, the reader is referred to the Web version of this article.)