Animal Behaviour 123 (2017) 21–32

Contents lists available at ScienceDirect

Animal Behaviour

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

Commentary

A novel approach for dominance assessment in gregarious species: ADAGIO

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ARTICLE INFO

Article history:
Received 3 May 2016
Initial acceptance 30 May 2016
Final acceptance 2 September 2016

MS number 16-00394R

Keywords:
aggression
behaviour
comparability
directed acyclic graph
hierarchy
linearity
nonlinearity
social rank
totality

The concept of social dominance has been used in a plethora of studies to assess animal behaviour and relationships between individuals for nearly a century. Nevertheless, a standard approach does not yet exist to assess dominance in species that have a nonlinear or weakly linear hierarchical structure. We amassed 316 published data sets and show that 73.7% of the data sets and 90.3% of 103 species that we reviewed do not have a strongly linear structure. Herein, we present a novel method, ADAGIO, for assessing the structure of dominance networks. ADAGIO computes dominance hierarchies, in the form of directed acyclic graphs, to represent the dominance relations of a given group of animals. Thus far, most methods for computing dominance ranks assume implicitly that the dominance relation is a total order of the individuals in a group. ADAGIO does not assume or require this to be always true, and is hence more appropriate for analysing dominance hierarchies that are not strongly linear. We evaluated our approach against other frequently used methods, I&SI, David's score and Elo-rating, on 12 000 simulated data sets and on 279 interaction matrices from published, empirical data. The results from the simulated data show that ADAGIO achieves a significantly smaller error, and hence performs better when assigning ranks than other methods. Additionally, ADAGIO generated accurate dominance hierarchies for empirical data sets with a high index of linearity. Hence, our findings suggest that ADAGIO is currently the most reliable method to assess social dominance in gregarious animals living in groups of any size. Furthermore, since ADAGIO was designed to be generic, its applicability has the potential to extend beyond dominance data. The source code of our algorithm and all simulations used for this paper are publicly available at http://ngonga.github.io/adagio/.

Social dominance is an attribute of almost all gregarious species and influences the cohesiveness, organization and behaviour of animals within a group (Chase, 1980; Hawley, 1999; Hemelrijk, 1998; Zinner & Wheeler, 2013). The original concept of social dominance was based on the consistency and directionality of aggressive behaviour and proposed that the establishment of dominance relations reduces conflicts in groups (Schjelderup-Ebbe, 1922). More recently, Drews (1993, p. 283) summarized the consistent criteria for dyadic dominance relations as: 'the pattern of repeated, agonistic interactions between two individuals, characterized by a consistent outcome in favour of the same dyad member and a default yielding response of its opponent rather than escalation'.

Dyadic dominance relations are often aggregated to dominance networks. Dominance hierarchies of dominance–subordination relations are then derived from these networks. Social rank and position in a dominance hierarchy often influence an individual's access to resources (Barrette & Vandal, 1986; Hirsch, 2011; Whitten, 1983), physiology (Buchanan, Evans, Goldsmith, Bryant, & Rowe, 2001), behaviour and interactions with others (Ellsworth & Belthoff, 1999; Newton-Fisher, Emery Thompson, Reynolds, Boesch, & Vigilant, 2010; Otten, Puppe, Kanitz, Schön, & Stabenow, 1999), reproduction (Cowlishaw & Dunbar, 1991; Ellis, 1995; Pusey, Williams, & Goodall, 1997) and overall fitness (Emlen & Oring, 1977; Schubert et al., 2007; Widdig et al., 2004). As such, the assessment of dominance relations and individual dominance status (rank) are essential components in the study of animal behaviour.

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http://dx.doi.org/10.1016/j.anbehav.2016.10.014
0003-3472/

Since the inception of ethology, researchers have developed various methods to analyse dominance relations (reviewed in: Bayly, Evans, & Taylor, 2006; Drews, 1993; Neumann et al., 2011; de Vries, 1998). An increased understanding of the complexity of social interactions has fostered the continued development of more complex methods in recent decades (Izar, Ferreira, & Sato, 2006; Schmid & de Vries, 2013). Most of the commonly used methods are based on the outcomes of dyadic agonistic or submissive interactions between group members. Observed interactions are then summarized in interaction matrices that represent the outcome of encounters over a defined period of time, e.g. I&SI (Schmid & de Vries, 2013; de Vries, 1998). Other methods are based on a paired comparisons paradigm (Kendall & Babington Smith, 1940), e.g. David's score (DS; David, 1987; Gammell, de Vries, Jennings, Carlin, & Hayden, 2003) and Elo-rating (ELO; Albers & de Vries, 2001; Elo, 1978). Although DS and ELO were originally designed to provide a measure of individual success, they are commonly used to obtain a rank order of individuals in a group.

One underlying assumption of almost all methods is that the dominance relations for a given group form a total order. Formally, this means that given any dyad (*A, B*), one can compare *A* and *B*. However, often this is not possible. A common problem in many empirical studies is that data pertaining to dominance relationships between group members is incomplete (Appleby, 1983; Garai, Weiss, Arnaud, & Furuichi, 2016). When interaction matrices contain structural and/or observational zeros, this results in unknown dominance relationships between a subset of individuals (Klass & Cords, 2011).

When a total order of individuals in a group does exist and the dominance relations are irreflexive, transitive and asymmetric (Izar et al., 2006; see Methods and Supplementary File S2 for definitions), then the dominance network is considered to be linear. However, dominance relations do not always fulfil the criteria for linearity, resulting in dominance hierarchies that are not perfectly linear. For example, a group of animals may have a pyramidal hierarchy if one or two individuals are dominant over several individuals of equal rank (Preuschoft & van Schaik, 2000). This particular type of hierarchical structure often occurs in wolf packs (van Hooff & Wensing, 1987).

To obtain a descriptive measure of the degree of linearity in dominance hierarchies, researchers frequently use Landau's linearity index (h; Landau, 1951). Landau's index obtains reliable results when information on dyadic relations is complete and when the group contains more than five individuals. The improved linearity index (h') corrects for ties and unknown relationships (de Vries, 1995). Consistent with other studies, we adopt the guideline that hierarchies with $h' > 0.90$ are considered to be strongly linear (Chase, 1974; Martin & Bateson, 1993). Although linearity is often considered to be the main structural characteristic of dominance relations, previous studies have suggested that the structure of the majority of observed data sets is not perfectly linear (e.g. Appleby, 1983; Jackson & Winnegrad, 1988). Herein, we compile and review 316 published data sets in which dominance relationships in 103 species were analysed, and investigate the degree of linearity in the structure of the data.

When the underlying assumptions of linear hierarchies are not met, the actual dominance structure of the study group is distorted, or inaccurately represented, by some methods. Since ordering individuals into a linear dominance hierarchy simplifies the complexity of a group's dominance relations, it may yield inaccurate results and unreliable dominance rank orders. The empirical evidence that many species do not have a linear dominance structure calls attention to the need for alternative methods to assess dominance relations in species and social groups that deviate from a linear hierarchical structure.

We present a novel approach, designated ADAGIO (approach for dominance assessment in gregarious species), to assess dominance relations. ADAGIO represents dominance hierarchies using directed acyclic graphs (DAGs; West, 2001). Formally, a DAG is a network that is free of cycles, i.e. a network where there is no path from one node (representing an individual) of the network back to the same node (individual). This means that there are no circular triads where individual *A* is dominant over *B, B* is dominant over *C*, but *C* is dominant over *A*. By using DAGs, ADAGIO is able to order individuals into nonlinear as well as linear structures. DAGs have long been used in computer science and mathematics (Speidel, Takaguchi, & Masuda, 2015) and as a tool for statistical inference (Jordan, 2004). More recently, they have been used in the field of genetics (Goeman & Mansmann, 2008; Roehner & Myers, 2014) and in analysing dominance networks (Izar et al., 2006; Shizuka & McDonald, 2012).

ADAGIO neither assumes nor requires that all individuals in a group are comparable with respect to dominance relations. For example, ADAGIO does not assume that given two individuals, *A* and *B*, one can assert that *A* is dominant over *B*, or that *B* is dominant over *A*. This assumption is inherent to most of the existing approaches, and is one of the key characteristics of linear hierarchies in which all individuals are indeed comparable. By discarding the assumption of totality, our approach provides a more accurate assessment of dominance relations, particularly for groups of animals wherein some dominance relationships are unknown.

Designed for gregarious species that do not have perfectly linear dominance hierarchies, ADAGIO is a systematic approach to extract a DAG from an interaction network. The resultant DAG is a graphical representation of the dominance structure of the given group. In this paper we (1) investigate the degree of linearity in dominance hierarchies of published studies and (2) assess the performance and accuracy of ADAGIO by comparing it with other frequently used methods. We validate the reliability of ADAGIO on empirical data obtained from published studies, and show that ADAGIO can be used to analyse hierarchies that range from completely linear to nonlinear in their structure. Finally, we discuss advantages and limitations of this new approach and its contribution towards an improved assessment of social dominance in group-living animals.

METHODS

Given a dominance network, current methods for dominance assessment compute a total order of the group. This is done either explicitly (e.g. I&SI) or implicitly through the assignment of comparable scores (e.g. ELO and DS). However, such a total order can fail to account for structural and observational zeros in the dominance network. For example, consider a dominance network that contains only the following interactions: (1) an individual *A* was dominant over individual *B* in three interactions, (2) *B* was dominant over *C* in two interactions and (3) *B* was dominant over *D* in one interaction. Existing approaches such as I&SI, ELO and DS would assign *D* a higher rank than *C* although no interaction between *C* and *D* was observed (observational zero) or was at all possible (structural zero). Such constellations are common in empirical data (see Results). Hence, our goal was to compute dominance hierarchies from dominance networks while refraining from assuming that the dominance relation is total.

Formally, assuming that the dominance relation is total is tantamount to assuming that dominance abides by the criteria of irreflexivity, transitivity, asymmetry and totality (Davey & Priestley, 2002) as explained below. Given that the assumption of totality is not always reflected in empirical data (e.g. due to observational or structural zeros in the dominance network, see Results), ADAGIO refrains from assuming that the criterion of totality holds. We are

thus left with the following characteristics for dominance relations: (1) irreflexivity: no individual is dominant over itself; (2) transitivity: if individual A is dominant over B and B is dominant over C, then A is dominant over C; (3) asymmetry: if A is dominant over B, then B is not dominant over A. (Note that asymmetry is a direct consequence of irreflexivity and transitivity.)

These characteristics translate to a type of relation known as a strict partial ordering, which can be characterized by DAGs. Hence, ADAGIO computes dominance hierarchies (in the form of DAGs) from dominance interaction networks. However, using DAGs instead of a linear structure to represent dominance has repercussions for the concept of ranks. So far, ranks have been assumed to be comparable entities, i.e. $rank(A) > rank(B)$ has commonly been understood to assert that A has a higher social status than B with respect to its dominance. However, the dominance relation being understood as a partial relation also implies that ranks derived from the DAG corresponding to a given group cannot be deemed comparable unless the DAG is fully linear. We thus extend the semantics of the concept of rank to be a measure that is comparable along the same lineage in a DAG and not comparable between lineages.

In the following, we explain our approach by means of a hypothetical example. A formal specification of ADAGIO, including a formal specification of the algorithm, is provided in File S2.

Overview of the Approach

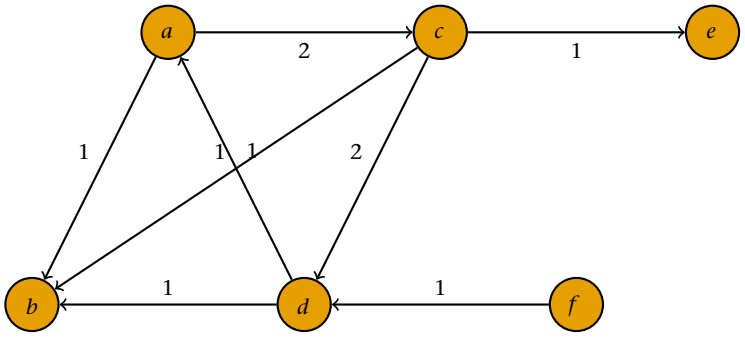
Given that the dominance relation is a strict partial ordering, ADAGIO aims to extract a dominance hierarchy in the form of a DAG from a given dominance network. If a dominance network G is not a DAG (i.e. if it contains cycles: circular triads or circular polyads), then adding edges to G will never get rid of cycles in G or lead to G being a DAG. Hence, ADAGIO aims to compute a dominance hierarchy from G by discovering the edges in G that should not be part of the DAG extracted from G. This problem translates to the feedback arc set problem (Karp, 1972). Known algorithms for finding the perfect solution to this problem have a runtime that can grow exponentially with the number of nodes in the input graph. As dominance networks can contain hundreds of nodes, we adopt a time-efficient, even if not optimal, approach to addressing this problem. In essence, ADAGIO begins by (1) copying the dominance network G to a graph H. Then, (2) it detects the largest strongly connected components (SCC) of H, i.e. the largest portions of the input graph (with respect to the number of nodes the portions encompass) that contain cycles. For example, let the network in Fig. 1 be a dominance network. The network contains exactly one SCC, which is the subgraph that contains the nodes a, c and d.

(3) If H is a DAG (i.e. if H does not contain any SCC), then ADAGIO terminates and returns H as the dominance hierarchy. (4) Else, ADAGIO's next step consists of omitting the edge(s) with the smallest weight that are contained in the SCCs detected in H. In our example, this is the edge from d to a with a weight of 1 (note that the other two edges in the SCC have a weight of 2). This leads to the graph shown in Fig. 2. The approach then goes back to step (2) and iterates between (2) and (4) until a cycle-free dominance hierarchy H has been constructed. In our example, the output graph is free of cycles after one iteration; hence ADAGIO returns the dominance hierarchy shown in Fig. 2. A key advantage of ADAGIO is that it is efficient and can be applied to graphs with thousands of nodes.

Preprocessing and Rank Computation

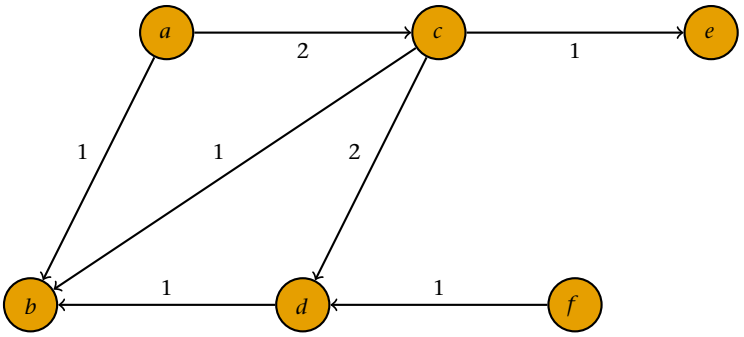
Our approach can be combined with a preprocessing approach derived from previous methods (e.g. I&SI, de Vries, 1998) that allows breaking symmetry at the dyadic level. For a given dominance network, the preprocessed weight of the edge between the individual A that appears dominant and the individual B that appears subordinate is set to the difference in the number of interactions won by A and the number of interactions won by B. The reciprocal edge is removed. For example, consider a dyad (A, B) where A won four interactions over B and B won three interactions over A. The processed weight of the edge from A to B would be $4 - 3 = 1$, while there would be no edge from B to A. In the case of a tie, both the edges from A to B and from B to A would not be considered in the further processing steps.

In addition to the preprocessing, we devised means to compute ranks from the dominance hierarchies computed by our approach. Many analysis models (e.g. generalized linear mixed models (McCulloch & Neuhaus, 2005)) require a numerical dominance value to be assigned to each individual of a group. Hence, we devised the following approach, dubbed top-down approach, to compute ranks from the result of ADAGIO. Given a dominance hierarchy H returned by ADAGIO, we begin by setting the rank of all the roots to $r = 1$. (Note that the roots of the DAG are individuals that are not dominated by other individuals within the dominance hierarchy.) In our example (Fig. 2), these would be the nodes a and f. We then assign the rank $r + 1$ to all direct children of nodes of rank r that do not yet have a rank iteratively. (A node B is a child of a node A if there is an edge from A to B.) By these means, we get the following rank assignment for the nodes in our example: $rank(a) = 1$, $rank(b) = 4$, $rank(c) = 2$, $rank(d) = 3$, $rank(e) = 3$ and $rank(f) = 1$ (see Fig. 3a). The converse approach, dubbed bottom-up approach and based on Shimoji, Abe, Tsuji, and Masuda (2014), leads to the following rank: $rank(a) = 1$, $rank(c) = 2$, $rank(f) = 2$, $rank(d) = 3$, $rank(e) = 4$ and $rank(b) = 4$ (see Fig. 3b). For a detailed



	a	b	c	d	e	f
a	0	1	2	0	0	0
b	0	0	0	0	0	0
c	0	1	0	2	1	0
d	1	1	0	0	0	0
e	0	0	0	0	0	0
f	0	0	0	1	0	0

Figure 1. Example of a hypothetical dominance network and corresponding interaction matrix. The nodes of the graph represent individuals in the group. The edges represent dominance interactions. An edge from x to y represents the observation of a dominance interaction where x is dominant over y. The numbers beside the edges represent numbers of dominance interactions. In the matrix, the rows represent winners of interactions and the columns represent losers.



$$\begin{array}{c} \\ a \\ b \\ c \\ d \\ e \\ f \end{array} \begin{array}{c} \begin{array}{cccccc} a & b & c & d & e & f \end{array} \\ \begin{pmatrix} 0 & 1 & 2 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 2 & 1 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \end{pmatrix} \end{array}$$

Figure 2. Output of ADAGIO for the running example. The edge from d to a is omitted by ADAGIO. This is reflected in the matrix returned by ADAGIO containing $(d, a) = 0$.

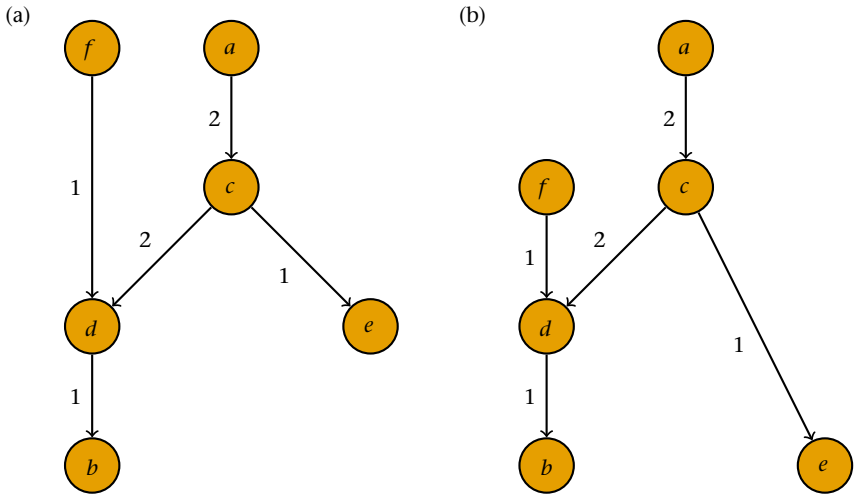


Figure 3. Output of ADAGIO showing the two rank computations. (a) Results of the top-down rank computation approach; (b) results of the bottom-up rank computation. The roots of the graph are a and f, which are both assigned a rank of 1 by the top-down rank computation. According to the bottom-up computation, $rank(f) = 2$.

formalization of the preprocessing and rank computation, see File S2. In the results and discussion sections of our paper, ADAGIO uses top-down rank computation while ADAGIO+b denotes the variation of ADAGIO with bottom-up rank computation. The same approaches used in combination with preprocessing are denoted ADAGIO+p and ADAGIO+b+p, respectively.

Therefore, the four versions of our approach include:

(1) ADAGIO: ADAGIO with top-down ranking;
(2) ADAGIO+p: ADAGIO with top-down ranking plus preprocessing;
(3) ADAGIO+b: ADAGIO with bottom-up ranking;
(4) ADAGIO+b+p: ADAGIO with bottom-up ranking plus preprocessing.

Evaluation Methodology

We evaluated our approach on empirical and simulated data (see File S2 for all details). The aims of the experiments on simulated data were to measure: (1) how well our approach reconstructed the ranks that led to the generation of a given dominance network (called ideal ranks); as well as (2) how well it performed when compared with other methods. In all experiments, we simulated the interactions by using the Bradley–Terry model (Bradley & Terry, 1952) as used in previous works (e.g. Boyd & Silk, 1983). In more detail, we generated simulated dominance networks as follows. For a group of size N, we first assigned a reference rank to each individual. While assigning these ranks, we ensured that we never generated a hierarchy that contained an individual of rank i (e.g. 3) as well as an individual of rank $i + 2$ (e.g. 5) but no individual of rank $i + 1$ (e.g. 4). The Bradley–Terry model underlying our experiments was configured to abide by either a linear probability model or an exponential model (with exponents 2, 3 and 4), which resulted in four different set-ups for the model. We experimented with group sizes of $N = 10$, 20 and 50 individuals. The numbers of interactions used were $2N$, $4N$, $8N$, …, $1024N$. For example, for groups of $N = 10$, we generated between 20 and 10 240 interactions. We ran each experiment (i.e. each combination of group size and number of iterations) 100 times. Overall, we thus generated 12 000 data sets and 57.3 million interactions.

In our first series of simulations, we measured the mean Euclidean distance between the rankings generated by the four variations of our approach and the reference ranking used during the generation. (Note that the Euclidean distance is not normalized to 1.) A smaller mean Euclidean distance means that the results of the approach more accurately matched the reference ranking used to generate the interaction matrix by means of the Bradley–Terry model. Hence, the smaller the mean Euclidean distance, the more accurate the ranking generated by the approach. The upper bound of the Euclidean distance for a simulated group is given by $\sqrt{N} - \frac{1}{\sqrt{N}}$, where N is the size of the simulated group. When $N = 10$, 20 and 50 individuals, the upper bounds are 2.85, 4.25 and 6.93, respectively. (More details on the upper bound are provided in File S2.)

To determine how much information our approach has to omit to generate a dominance hierarchy, we measured the difference in the amount of information contained in empirical dominance

networks and the corresponding dominance hierarchies computed by ADAGIO. We computed the proportion of the total number of interactions that were not included in the DAGs computed by ADAGIO from empirical data sets after the preprocessing by using a measure known as the relative error and defined as follows: let M' be the preprocessed interaction matrix given to ADAGIO as input and let Z be the matrix of the dominance hierarchy returned by ADAGIO. Then, ADAGIO's relative error is:

$\frac{||M'-Z||}{||M'||}$, where $||X|| = \sum_{i,j=1}^{n} x_{ij}$ for any matrix X.

For our running example, the input matrix is as shown in Fig. 1. ADAGIO returns the matrix shown in Fig. 2 by discarding the edge from d to a during the construction of the DAG. This leads to a relative error of $\frac{1}{10} = 10\%$.

RESULTS

Results on Simulated Data

Comparison of the four variations of ADAGIO

The four variations of our approach achieved similar results over all of the simulations (see Fig. 4). ADAGIO+b+p (i.e. ADAGIO with bottom-up rank computation and preprocessing) and ADAGIO+b performed best (i.e. achieved the smallest mean Euclidean distance from the ideal ranking) when faced with a small number of simulated interactions, which was in line with the number of interactions and the group sizes of the empirical data we gathered for this study (see File S2 for more details). We thus compared the other approaches with ADAGIO+b+p.

Comparison with other approaches

Given the results of the four variations of ADAGIO (see Fig. 4), we compared ADAGIO+b+p with I&SI, ELO and DS (Fig. 5). The results show that the Euclidean distance of the ranking generated by ADAGIO+b+p to the ideal ranking was significantly smaller than the distance of the ranking generated by the other three methods to the ideal ranking across all simulation settings and for all groups of $N = 10$, 20 and 50 individuals (e.g. for I&SI and a group of 50, paired-samples t test: $t_{1995} = -41.16$, $P < 0.0001$). This result also holds when the asymptotic behaviour of the approaches is considered (see File S2, Fig. S7).

Results on Empirical Data

Our review of 316 published data sets (Table S1) revealed a wide range in the linear structure of dominance data. The improved Landau index (h') ranged from 0 to 1 (Fig. 6). Overall, 73.7% ($N = 233$) of the reviewed data sets had a weakly linear or nonlinear dominance structure ($h' < 0.90$). Furthermore, 93 of the 103 reviewed species (i.e. 90.3%) had at least one data set with a weakly linear or nonlinear structure.

The goals of our analyses on empirical data were threefold: (1) quantify how much information ADAGIO omits from graphs to compute DAGs; (2) assess whether our approach can be used on linear data; and (3) demonstrate the scalability of our approach.

Information Omitted From Empirical Data

The distribution of relative error achieved by ADAGIO on empirical data shows that ADAGIO omits less than 10% of the information for more than 86.5% ($N = 238$) of the 275 input data sets. For more than 94.5% ($N = 260$) of the data sets, ADAGIO removed less than 20% of the total edge weight to generate a DAG. The outliers ($N = 15$) are data sets with matrices that contain large strongly connected components (SCCs), e.g. the data set dubbed Langbein & Puppe 2004-D with an SCC size of 9. A detailed assessment of the information omitted by ADAGIO is provided in File S2.

Results on Linear Data

We tested the performance of our approach on linear data by applying ADAGIO+b+p to 41 empirical data sets with $h' = 1$. In 37 data sets where all individuals were comparable under the assumption of dominance being transitive (i.e. data sets with $h = 1$), ADAGIO+b+p returned the same linear hierarchy as ELO and DS. In the four data sets (see Fig. 7; Archie, Morrison, Foley, Moss, & Alberts, 2006; Bell & Gorton, 1978; Harcourt, 1979; Watt, 1986) in which this condition did not hold ($h' = 1$ and $h < 1$), ADAGIO did not return a total ordering because the interaction matrices contained too many zeros, rendering certain individuals incomparable. Since ADAGIO detects a linear hierarchy if it exists, but does not make individuals comparable that are not comparable according to the input data, we regard the results of ADAGIO to be correct on all 41 data sets. Fig. 8 shows further examples of hierarchies generated by our approach.

Scalability

We evaluated the scalability of our implementation by measuring the runtime required on a 64-bit i7 (2.3 GHz) laptop running Windows7 SP1. The results indicate that our implementation required less than 10 ms per data set. This suggests that our approach scales well.

DISCUSSION

ADAGIO represents dominance relations and the structure of a group's dominance hierarchy using a DAG. It is a systematic approach to detect the underlying structure of dominance networks that range from nonlinear to perfectly linear. It computes nonlinear and partial dominance hierarchies from dyadic dominance interaction data, preserves as much information from the original data as possible, refrains from assuming that all members of the group can be compared, and refrains from adding additional information in the graph. ADAGIO generates a graphical representation of a group's dominance structure that clearly depicts different dominance ranks and the number of unique lineages (i.e. distinct and ordered paths from a root or node through all comparable individuals; Izar et al., 2006). Hence, dominance relationships are rendered in a highly informative manner. Since ADAGIO is generic, time-efficient and versatile, it can extract a DAG from any dominance network or directed graph.

Strongly Linear Hierarchies are not the Norm

Our literature review of dominance data spanning 103 animal species revealed that the majority of data sets and species that we analysed did not have a strongly linear dominance hierarchy. These findings corroborate previous studies that suggested that perfectly linear dominance hierarchies are unlikely to occur by chance (Chase, Tovey, Spangler-Martin, & Manfredonia, 2002) and are not common, especially when group size is large (e.g. >10 individuals; Appleby, 1983; Jackson & Winnegrad, 1988; Jameson, Appleby, & Freeman, 1999). Possible explanations for this include species lacking ritualized or formal signals of dominance, infrequent interactions among individuals, structural zeros, insufficient sampling effort or incomplete observations by researchers (e.g. observational zeros), or that the group's structure simply is not linear. Furthermore, researchers may not be able to perceive or understand some signals of

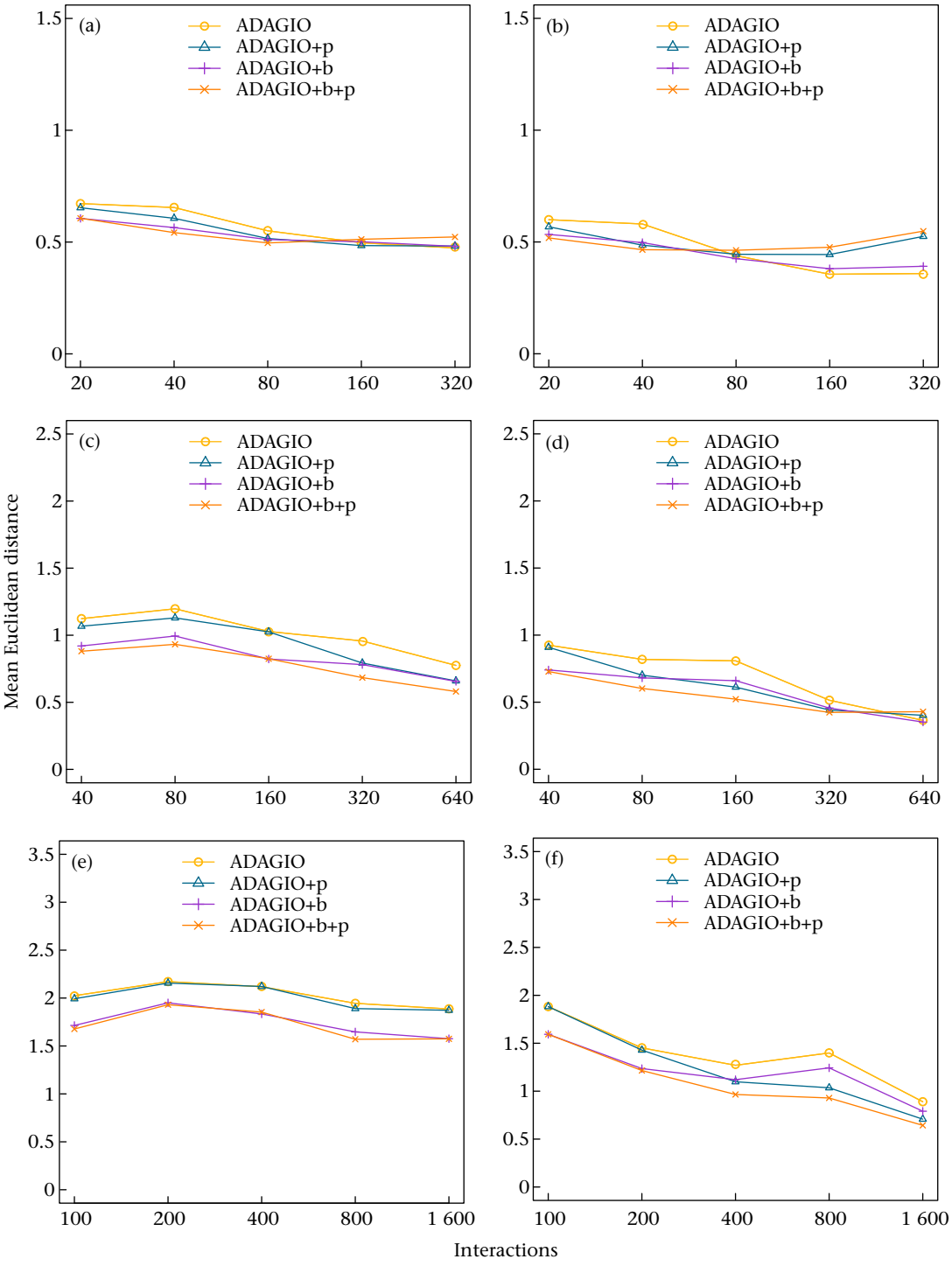


Figure 4. Comparison of the four variations of ADAGIO on simulated data. (a) Linear simulation, 10 individuals; (b) exponential simulation, 10 individuals; (c) linear simulation, 20 individuals; (d) exponential simulation, 20 individuals; (e) linear simulation, 50 individuals; (f) exponential simulation, 50 individuals.

dominance, e.g. body postures (van Hooff & Wensing, 1987) and pheromones (Kou, Chang, Chen, & Ho, 2009).

Although linearity is often reported in studies, it is not always demonstrated objectively. In some cases, authors describe the dominance hierarchy as linear, but report triangular relationships or other internal inconsistencies within the hierarchy. In other studies, despite unknown relationships between group members, individuals are arranged in a linear order with the objective to minimize instances of individuals dominating others higher in rank (Schein & Fohrman, 1955). These methods obscure irregularities in dominance hierarchies and increase the overall impression of linearity in groups that actually do not have a linear structure (Appleby, 1983; Beilharz & Mylrea, 1963).

In sum, dominance hierarchies with linear structures appear to be less prevalent in animal groups than was once assumed. This further highlights the need for approaches like ADAGIO that analyse partial orders without forcing group members into a ranked list of individuals.

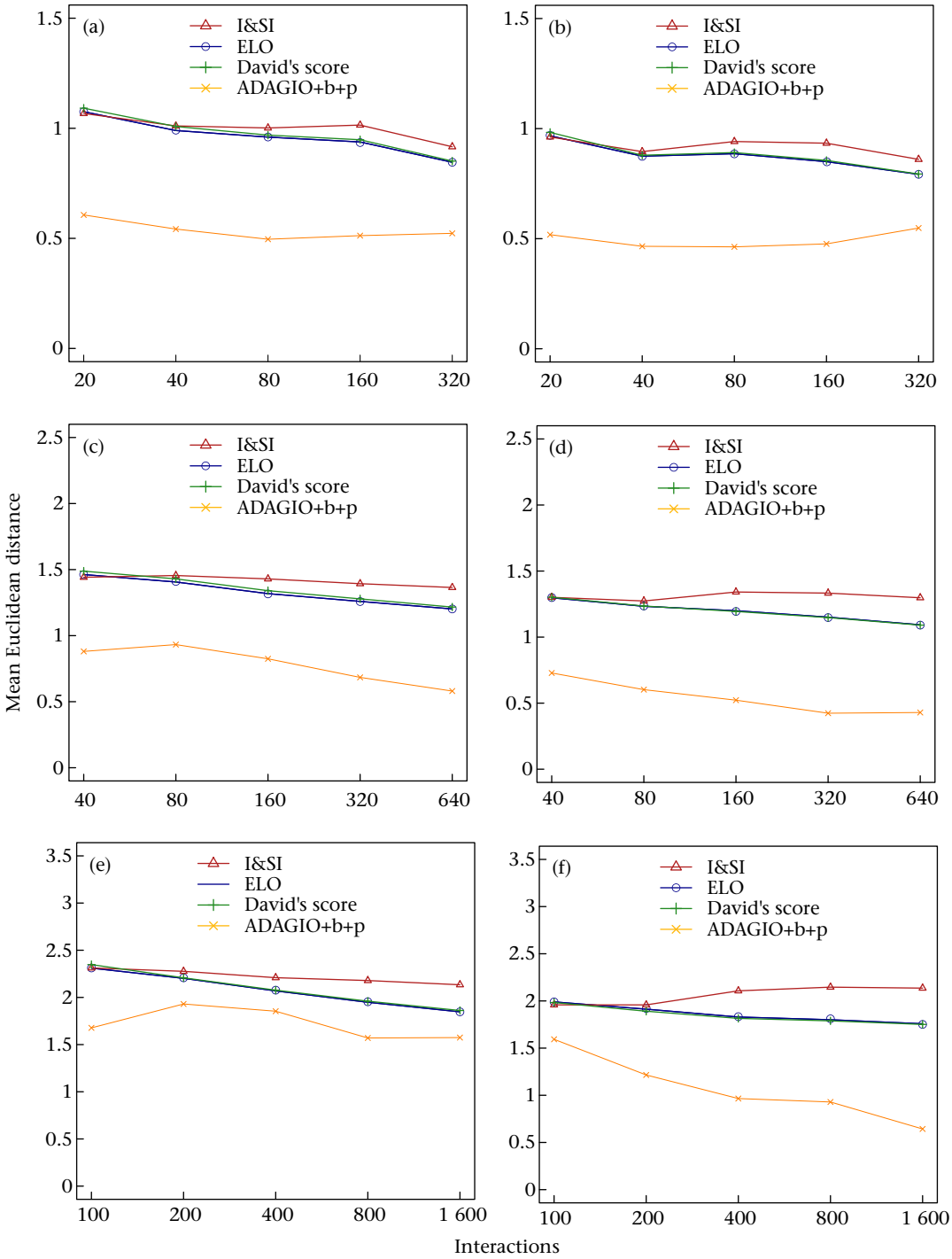


Figure 5. Comparison of ADAGIO on linear and exponential simulated data ($x = 2$). (a) Linear simulation, 10 individuals; (b) exponential simulation, 10 individuals; (c) linear simulation, 20 individuals; (d) exponential simulation, 20 individuals; (e) linear simulation, 50 individuals; (f) exponential simulation, 50 individuals.

Variations of ADAGIO

The results suggest that our approach performed best on exponential data as it reached its break-even point with a smaller number of interactions (Fig. 4). When the number of interactions was limited (e.g. <100), ADAGIO+b+p and ADAGIO+b had the smallest average error. As the number of interactions increased, ADAGIO and ADAGIO+b performed better. Overall, the results of the simulations revealed that ADAGIO is significantly better than the other variations across the three group sizes tested. Users should consult Fig. 4 when deciding which variation of ADAGIO to use (e.g. top-down or bottom-up rank computation), and select the most appropriate variation based on the number of individuals and the number of interactions in their data set.

ADAGIO Compared with Other Methods

In our experiments on simulated data, the ranking generated by ADAGIO+b+p matched the true reference ranking better than I&SI, ELO and DS across all simulations (i.e. ADAGIO+b+p led to a

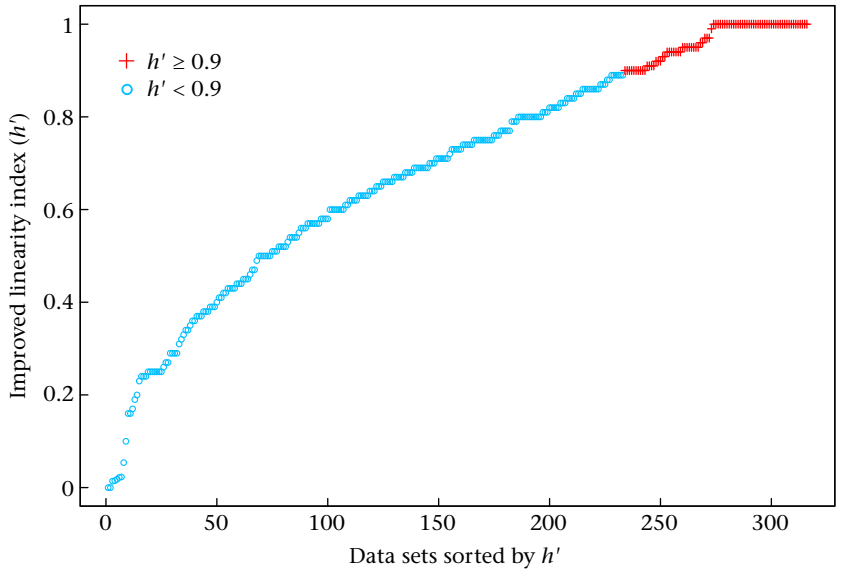


Figure 6. Improved linearity indices of 316 reviewed data sets. Data sets in red have a strongly linear structure.

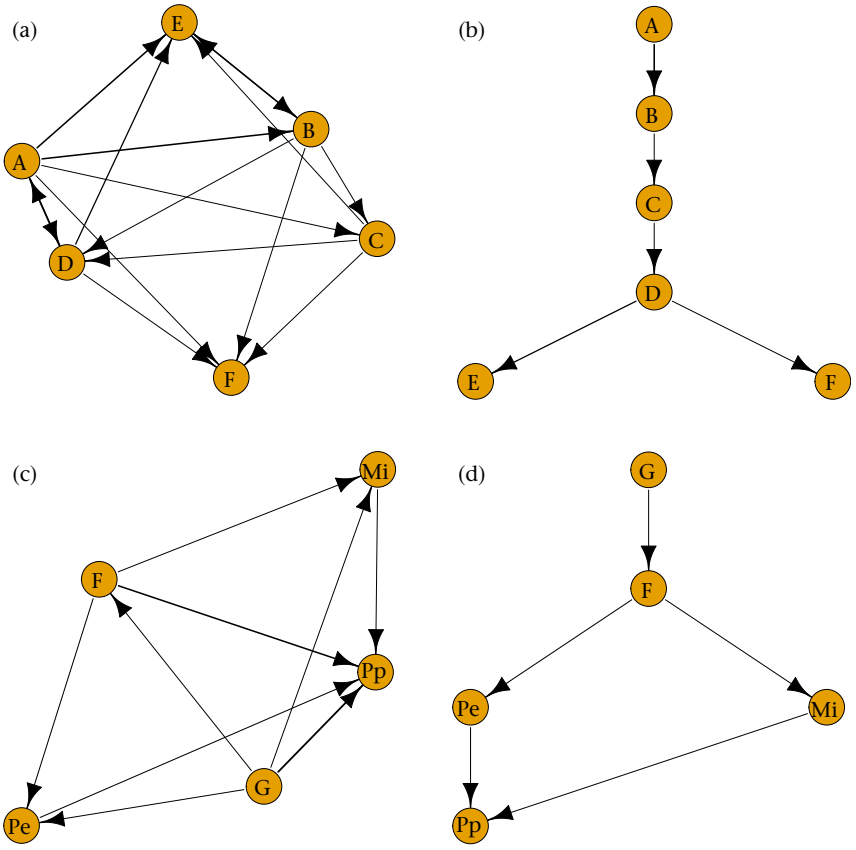


Figure 7. Examples of nonlinear outputs generated by ADAGIO+b+p for empirical data sets with $h' = 1$. (a, c) The original data. (b, d) The results returned by ADAGIO+b+p. The thickness of the edges (lines) grows linearly with their weight. (a) Archie-2006-CB (Archie et al., 2006); (b) directed acyclic graph returned by ADAGIO on Archie-2006-CB. The nodes *F* and *E* are not comparable in the original data. $rank(A) = 1$, $rank(B) = 2$, $rank(C) = 3$, $rank(D) = 4$, $rank(E) = rank(F) = 5$. (c) Harcourt-1979-1 (Harcourt, 1979); (d) results of ADAGIO on Harcourt-1979-1. Nodes *Mi* and *Pe* are not comparable in the original data. $rank(G) = 1$, $rank(F) = 2$, $rank(Pe) = rank(Mi) = 3$, $rank(Pp) = 4$.

significantly smaller mean Euclidean distance than the other methods). ELO and DS were comparable in their performance, and all methods performed better than I&SI. Interestingly, the difference in performance grew with the size of the group as shown in Fig. 5. Our results on empirical data show that ADAGIO accurately processes nonlinear data (i.e. data with $h' < 0.9$). Additionally, ADAGIO performs as well as, or better than, the other three methods when $h' > 0.9$. These results are of great importance, as

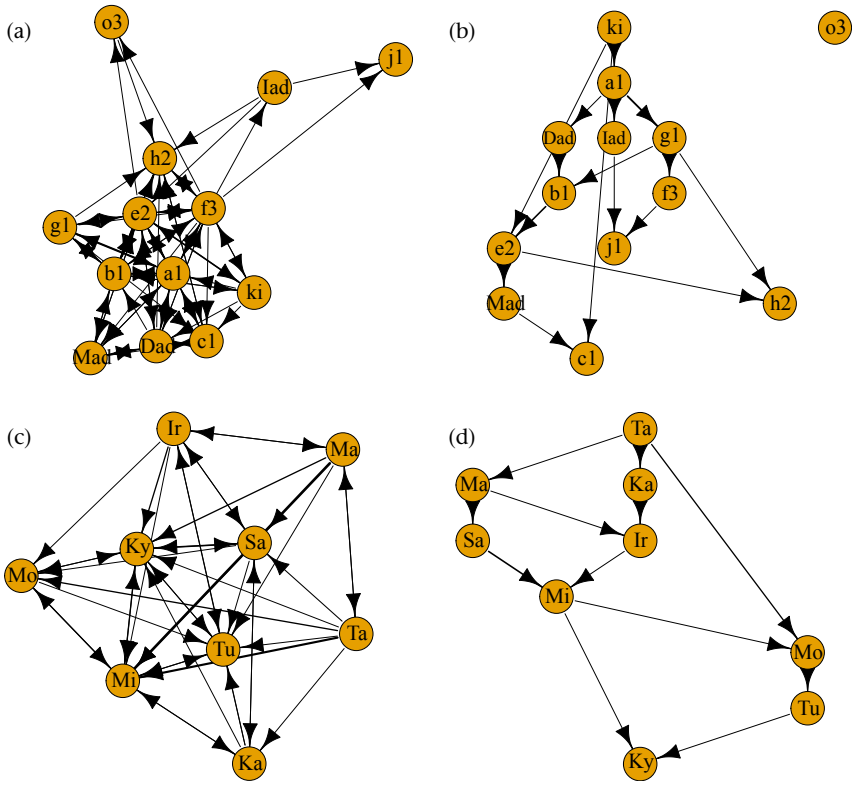


Figure 8. Examples of outputs generated by ADAGIO+b+p. (a, c) The original data. (b, d) The results returned by ADAGIO+b+p. The thickness of the edges (lines) grows linearly with their weight. (a) Kolodziejczyk2005-1 (Kolodziejczyk, Kloskowski, & Krogulec, 2005), $h = 0.15$; $h' = 0.24$. (b) Results of ADAGIO on Kolodziejczyk2005-1. (c) Korstjens2002-1 (Korstjens, Sterck, & Noë, 2002), $h = 0.79$; $h' = 0.83$. (d) Results of ADAGIO on Korstjens2002-1.

they suggest that ADAGIO can be used to assess dominance relations independently of the degree of linearity in the hierarchy underlying the species of interest.

While some other approaches (e.g. Izar et al., 2006; Shimoji et al., 2014) also use DAGs to describe the organization of dominance relations, they do not provide algorithms that allow researchers to perform a global assessment of the dominance hierarchies in species. In particular, the method proposed by Izar et al. (2006) requires an input node from the interaction network as a parameter. This node is then used to compute a DAG that represents the given interaction network from the perspective of the input node. Hence, their method allows researchers to assess a network from the local perspective of a given individual and not from a global perspective like ADAGIO. Shimoji et al. (2014) preprocessed interaction matrices manually to generate DAGs by deleting edges. While they did propose the bottom-up approach for assessing dominance, also used herein, our simulations suggest that ADAGIO asymptotically performs best with the top-down rank computation approach.

Main Advantages of ADAGIO

Accuracy and versatility

When a strongly linear dominance hierarchy can be derived from the interaction matrix, ADAGIO returns the same results (e.g. individual ranks) as other methods. However, our results on empirical and simulated data show that ADAGIO computes more accurate dominance ranks, with respect to the mean Euclidean distance chosen in our experiments, than other frequently used methods when analysing data that have a nonlinear structure. Consequently, ADAGIO is a versatile approach that can be used to accurately analyse the structure of dominance in both linear and nonlinear data.

Unknown dyadic relationships are not overwritten or ignored

When methods fulfil the assumption of comparability by including predicted dominance outcomes from unobserved interactions, information within observational zeros is not preserved. Concealing unknown relationships may obscure important information regarding the social structure of the group. Other studies have cautioned against overwriting or ignoring unknown relationships, reporting that the pernicious effects of doing so include incorrect estimates of steepness and linearity indices (Appleby, 1983; Klass & Cords, 2011; Norscia & Palagi, 2015). Dominance should not be assumed, but should be deduced from observed interactions (Barrette & Vandal, 1986). By refraining from introducing additional data based on predicted outcomes into the interaction matrix, ADAGIO preserves observational and structural zeros. Since ADAGIO does not compare dyads lacking dominance interactions, the resultant plot shows both comparability and noncomparability between individuals. Hence, ADAGIO produces a transparent, graphical representation of all known relationships, and does not amplify a linear structure within weakly linear groups.

Observational zeros do not affect ADAGIO's performance

Sparse data sets are problematic with some of the commonly used approaches, e.g. the I&SI method. Since some methods do not always yield reliable results when there are many empty cells in the interaction matrix, observational zeros can negate the use of these methods (Cafazzo, Valsecchi, Bonanni, & Natoli, 2010; Poisbleau, Jenouvrier, & Fritz, 2006; Schmid & de Vries, 2013). In contrast, ADAGIO's analysis of observed interactions was not affected by unknown relationships.

No minimum or maximum number of individuals

Methods that are based on a linear hierarchy structure require completeness (Izar et al., 2006), and therefore may not accurately

assess dominance in large groups of individuals. Since ADAGIO computes a partially ordered set, the requirement of completeness does not need to be fulfilled. Consequently, there are no constraints with respect to the maximum number of individuals that can be analysed using ADAGIO. On the other hand, if there are fewer than six individuals in the interaction matrix of a given group, Landau's linearity index will not yield statistically significant results (Landau, 1951; de Vries, 1995). This requirement for a minimum of six individuals precludes the use of some methods when assessing small groups. With no restrictions in terms of the minimum or maximum number of individuals required, ADAGIO is a versatile approach that can assess dominance in animal groups of any size.

Dominance ranks generated systematically for nonlinear and linear data

Variation in the structure of dominance hierarchies occurs not only among species but also within species. For example, consistent intersexual differences characterize the structure of dominance in several species. Often males have a strongly linear dominance hierarchy, while females have only a weakly linear or partial hierarchy (e.g. Komers, 1989; Stevens, Vervaecke, de Vries, & van Elsacker, 2007). Common reasons for this disparity are infrequent conflicts among females, low rates of aggressive behaviours, nonaggressive strategies to solve conflicts and the rarity of formalized signals of dominance (Isbell & Young, 2002; Wheeler, Scarry, & Koenig, 2013). Consequently, when exploring the relationship between dominance status and certain behaviours, researchers often assign females to rank categories (Murray, 2007; Pusey et al., 1997), or compare the behaviour of individuals with a clear social status to all other individuals (Hohmann & Fruth, 2000). An important advantage of ADAGIO is that it is a systematic approach to calculate the rank of each individual relative to the alpha individual(s). Hence, the resulting ranks are not derived arbitrarily.

Open-source and user-friendly implementation

ADAGIO is open-source and was designed to be easy to use. In particular, the implementation solely requires an interaction matrix as input to be run in the default mode. Optional parameters allow one to select a particular variation of ADAGIO. The results of ADAGIO are provided both in graphical and textual form. In addition, the implementation returns: (1) Landau's linearity index (h) and the corrected Landau's index (h') for the input data; (2) error scores that quantify the amount of information that was removed from the input matrix to generate a DAG; (3) the directional consistency index (DCI; van Hooff & Wensing, 1987); and (4) the results for alternative methods such as I&SI, DS and ELO. The implementation comes with a manual that explains the results of the implementation.

Limitations and Future Considerations

Although ADAGIO performs well in our experiments, it still has a few limitations. First, the error rate of our approach increases when provided with a very large number of interaction simulations. This is due to ADAGIO making more suboptimal decisions when removing edges from the input graph when a large number of interactions are monitored. However, this behaviour does not seem relevant when processing empirical data sets, as our simulations suggest that it only occurs when the input data comprise a very large number of interactions. We will address this drawback in future by combining our approach with approximate solutions for NP-complete problems (e.g. Baker, 1994).

While our results show that ADAGIO+b+p should be used in most studies with a limited number of interactions, users could choose a more pragmatic approach by simply running all versions of our approach when selecting the version that removes the smallest amount of information. A predictive analysis of the behaviour of our approach could also allow researchers to detect the appropriate variation of ADAGIO to use on a given data set. For example, one could envisage running simulations to generate a graph similar to the input graph. The ADAGIO variation that produced the best results on the simulated graph would then be used on the empirical graph. While such an approach might reduce the scalability of ADAGIO, it could increase its usability.

Finally, our approach (as presented herein) does not deal with the temporal aspect of dominance and assumes a static interaction network. This drawback of the approach can be addressed by extensions akin to those used in evolutionary graph clustering (see, e.g. Chakrabarti, Kumar, & Tomkins, 2006).

Conclusions

Dominance ranks are often used to predict the social behaviour and interactions of individuals. Consequently, an incorrect assignment of individual ranks could negatively affect conclusions that are drawn with respect to the relationship between social rank, physiological or behavioural measures and fitness. Furthermore, an inaccurate assessment of a group's social structure could affect the assessment of relationships within the group. We have shown that ADAGIO can be used to assess dominance relations in animal species ranging from insects to fish, and from birds to mammals, with a higher accuracy than existing approaches commonly used for this purpose. In future work, we will improve upon the algorithm underlying ADAGIO, e.g. by using integer linear programming (Garfinkel & Nemhauser, 1972).

Acknowledgments

This work was funded in part by the Max Planck Society and by a grant from the Deutsche Forschungsgemeinschaft (HO-1151/9-1). We gratefully acknowledge Barbara Fruth, Roger Mundry, Liza Moscovice, Martin Surbeck, Niina Nurmi, Jeroen Stevens and Verena Behringer for fruitful discussions, and thank Liza, Martin and Niina for providing data from wild bonobos to test and refine the algorithm. We thank many authors listed in Table S1 who provided raw data in the form of interaction matrices for inclusion in our analysis. We are grateful to Roger Mundry for help with the simulation experiments, and sincerely thank Roger, Frances D. Burton, Martin Surbeck, Mimi Arandjelovic and two anonymous referees for helpful comments on the manuscript.

Supplementary Material

Supplementary material associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.anbehav.2016.10.014.

All data sets used for this study were derived from existing literature (see Table S1). The source code for ADAGIO (including the code for the simulations) can be found at http://ngonga.github.io/adagio and is available under the GPLv3 licence.

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