Original Article

# Comparative transitive and temporal orderliness in dominance networks

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Dominance is a social relation between a subordinate animal and the dominant to which it submits. Animal groups seem regularly to form dominance hierarchies in which dominance relations are transitive and stable, but comparative studies are rare. Dominance hierarchies can be formalized as social networks, with arrows (*directed edges*) pointing from dominant animals (*nodes*) to subordinates. Using this network perspective, we explored the orderliness of 40 published datasets for taxa from ants to elephants. To quantify orderliness, we used the *triad census*, a technique from sociology, that enumerates the proportion of orderly (transitive) triads (e.g., *A* dominates *B* and *C*, *B* dominates *C*, yielding clear top, middle, and bottom rankings) versus disorderly (cyclic) triads (e.g., *A* dominates *B*, *B* dominates *C*, but *C* in turn dominates *A*). All 40 datasets showed a significant excess of orderly (transitive) triads and a deficit of disorderly (cyclic) triads compared with the null model of random networks. Most datasets showed relatively high rank stability (mean stability index of 0.81 on a scale from 0 to 1). Steep hierarchies arise when the scores used to rank contestants differ sharply, further promoting stability. All 40 dominance hierarchies were steeper than expected from randomized sequences of contests. The overwhelming conclusion was that animal groups are orderly, as assessed by a high proportion of transitive relations, a paucity of disorderly cycles, and high temporal stability in rankings. Thus, a certain degree of self-organization may characterize even agonistic interactions across many different kinds of animal societies. *Key words:* orderly, self-organizing, social network, triad census. *[Behav Ecol]*

## INTRODUCTION

From molecules to societies, nature is often (surprisingly) patterned and orderly. Although order is obviously crucial for systems such as DNA replication, it is less obvious why animal societies consisting of competing individuals should be orderly. In particular, biologists have long noted that dominance hierarchies are surprisingly transitive (sometimes termed "linear") (Landau 1951; Dawkins 1976; Lindquist and Chase 2009). Maynard Smith (1983), from a more general perspective, felt that orderly queues in nonhuman societies posed a significant evolutionary puzzle, because lower ranking animals should usually have strong incentive, and little disincentive, to disrupt the queue—any shuffle would be unlikely to worsen their lot, and might help it. He argued that external enforcement, such as the presence of police, would be required, and thought it unlikely that nonhuman animal societies would exhibit any structures for external enforcement. After being unable to create models with winner–loser effects sufficiently strong to explain the orderliness of dominance hierarchies, Lindquist and Chase (2009) proposed that the observed orderliness requires that "members of groups are *intensely* aware both of their own interactions as well as interactions occurring among other members of their

group" (emphasis in the original). Regardless, nonhuman animal groups often form orderly hierarchies.

Dominance is fundamentally a *relation* between 2 individuals (Bernstein 1981), whereby, after 1 or more contests or interactions, 1 individual assumes the dominant role and the other the subordinate role. Indeed, characteristic submissive behaviors that terminate a conflict (Chase 1980) may be the essential determinant of the relation (Rowell 1974). The mechanics of how the relation is established, and the various costs and benefits of high dominance rank, can vary widely among species (Ellis 1995). Dominance data are usually presented as a table or matrix of contests or interactions, in which the members of the group are listed in both the rows and columns, with wins shown in the rows and losses in the columns. Any such matrix or table is directly equivalent to the adjacency matrix, a standard input form for social network data (Wasserman and Faust 1994; see p. 153 for extension of the adjacency matrix concept from binary to weighted matrices), meaning that dominance data are naturally amenable to analysis as a social network. A dominance network then consists of *nodes* (animals; the number of nodes is therefore the size of the group included in the dominance dataset) and directed *edges* (arrows pointing from winner to loser). The bidirectional edges of this *contest matrix* will be weighted by the number of contests won by the contestant at the source of the edge (arrow). Despite the natural emphasis on the observed contests, dominance/subordinance is fundamentally a yes/no relation, so a natural extension of the network perspective is to consider an *outcome matrix* that denotes the 0/1 dominant–subordinate relation for each dyad. The outcome matrix will be binary (0/1) and directed,

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with 1-way edges pointing from dominant to subordinate. The individual winning the majority of contests for each dyad in the contest matrix receives a 1 in the outcome matrix, the majority loser a 0 (Chase 1980). One can assess the stability of dominance relations by determining how the structure of those relations (i.e., the outcome network) is affected by the time ordering of its constituent contests.

A fundamental component of any network is the triad, a set of 3 nodes (Faust 2007, 2010). A network with *n* nodes has *n-choose-3* triadic combinations of individuals, and classifying the types of possible triads has long been a feature of the sociological network literature (Holland and Leinhardt 1976). In a recent meta-analysis (Shizuka and McDonald 2012) of 101 published dominance datasets, we confirmed the striking orderliness of hierarchies, in terms of their relative lack of cyclic or nontransitive relations (e.g., a triad in which *A* dominates *B*, and *B* dominates *C*, but which becomes cyclic and disorderly if *C* dominates *A*; Figure 1). Dominance dynamics may, therefore, join the growing evidence for varying degrees of self-organization in nature (Camazine 2001; Couzin and Krause 2003).

In this study we assess, in more detail, the orderliness of dominance hierarchies from social network and other perspectives, using 40 published datasets. We prefer the term *orderliness* to *linearity* because it is more inclusive, and because it avoids conflation with the most widely used "linearity" metric (de Vries 1995), derived from the work of Landau (1951), which we show (Shizuka and McDonald 2012) to be inevitably biased toward underestimating transitivity. The bias toward underestimating orderliness in the de Vries metric, which we avoid by assessing transitivity (Shizuka and McDonald 2012) rather than "linearity," arises from the necessity for random imputation about unknown relations (null dyads). Null dyads are those in which individuals do not establish a dominance relation, perhaps because of insufficient observer effort, or, more interestingly, because of active avoidance based on third-party observer effects (Oliveira et al. 1998). For technical reasons (reviewed in de Vries 1995), null dyads complicate the assessment of Landau's (1951) linearity index. Unfortunately, random imputation of the outcomes of null dyads creates a potentially problematic side effect, especially for sparse networks. In random directed networks, which often serve as null models against which to assess observed networks (Wasserman and Faust 1994), the proportion of triangles (triads with all 3 edges present) that are *transitive* (*A* dominates *B* and *C*, *B* dominates *C*) is only 0.75 (Faust 2010) and fully 0.25 are intransitive *Cycles* (no clear dominant, as described in the previous paragraph). Empirical dominance data, viewed as networks, rarely show anywhere close to a proportion of 0.25 intransitive *Cycles* (Shizuka and McDonald 2012). Thus, random imputation forces disorder into systems that may otherwise be highly orderly. We further prefer the term *orderliness* because it captures both the ability to ordinate

animals from most to least dominant, and the temporal stability of that rank order.

As we use the term, therefore, orderliness depends on 3 emergent features: 1) transitivity ("linearity"), 2) stability (frequency of rank change over time), and 3) rank steepness (disparity in rank scores—steep hierarchies mean upsets are less likely to cause overall rank changes). Metrics useful for assessing our 3 criteria for the orderliness of dominance hierarchies include the proportion of transitive versus cycle triads, readily implemented via the network technique known as the *triad census* (Holland and Leinhardt 1976), rank scores (as a basis for ordination), the temporal stability of the rank ordering, and the steepness of the hierarchy, meaning the differences among the scores used to determine ranks. Although numerous dominance ranking schemes exist, Elo rating, a rank-score system derived from chess, has the huge advantage of dealing very well with "missing" data (dyads that do not interact), is implemented (dynamically) from the simple time-ordered sequence of dyadic outcomes, and is readily assessed for temporal stability (Neumann et al. 2011).

Although orderliness is an emergent property of a group or society, individuals can clearly play pivotal roles in speeding or slowing the emergence of order. Analyses of temporal sequences of social network configuration have provided useful insights into the importance of network position as a predictor of reproductive success for individuals (McDonald 2007). Likewise, social network approaches have proved useful for identifying individuals that may play a key role in promoting (Flack et al. 2006) or reducing the orderliness of social groups. A key concept in social network theory is node *centrality*, the extent to which a node is connected to other nodes in the network (Wasserman and Faust 1994). Centrality is most simply assessed as *degree*, the number of nodes to which a given node is directly connected. Many other metrics exist for assessing centrality, including *betweenness* and *eigenvector centrality* (Wasserman and Faust 1994, p. 169). These various centrality metrics can help identify individuals that, despite their pivotal role, may not be obviously high ranking or successful. The involvement of individuals in particular triad types in the triad census can help uncover such pivotal individuals. For example, for networks with several cycles, one could ask whether particular individuals are overrepresented in cycle membership. If so, one could ask whether those individuals also show high levels of centrality from a social network perspective. In that case, their disappearance or removal could result in a reduction in cyclicity, as well as in major changes in network structure and even function, as found for high-ranking primates by Flack et al. (2006).

In a series of pioneering studies, Chase (e.g., 1985) used a "jigsaw puzzle" and triadic approach to study the sequences of dominance interactions. In this study, we build on that research, by proposing that tracking of the ontogeny of dominance contests in the explicitly social network approach of,
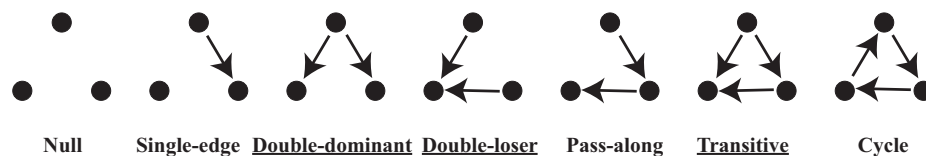


**Null    Single-edge    Double-dominant    Double-loser    Pass-along    Transitive    Cycle**

**Figure 1**
The types of triads possible when asymmetric *edges* (1-way arrows pointing from dominant to subordinate) join *nodes* (animals). Any network containing *n* nodes has *n-choose-3* triads. Each of the *n-choose-3* triads can be classified as 1 of the 7 distinct (nonisomorphic) triad types shown above. The count of triad types is called a *triad census*. The inherently transitive (orderly) types, *Double-dominant*, *Double-loser*, and *Transitive*, are underlined. The 2-edge triad type that we term *Pass-along* can become either cyclic (disorderly; if the third edge points up) or transitive (orderly; if the edge points down), if and when the third edge (dominance relation) is established.

for example, the triad census, should allow researchers to examine and experiment with sequences of interactions and their causes and consequences, within a rich theoretical framework. We assess patterns of order and disorder in our set of 40 published datasets from the perspective of transitivity, the stability and steepness of rank hierarchies, and the pattern of involvement of individuals in cycles, because cycles are a fundamental source of disorder in dominance hierarchies. If orderliness prevails, then transitivity should be high relative to a null model based on comparison with random directed networks, the hierarchies should be relatively stable across sequences of contests, and the scores that determine rank orderings should drop steeply across the hierarchy. If certain individuals play a pivotal disorder-inducing role in those groups that are less orderly (have more cycles), then we should expect that they would be overrepresented in cyclic relations.

## MATERIALS AND METHODS

### Empirical datasets

We analyzed 40 published datasets (Appendix 1) that measured dominance contests among conspecific animals. With 4 exceptions, the datasets were a subset of a larger sample of 101 datasets used for a meta-analysis (Shizuka and McDonald 2012) of patterns of transitivity (linearity) in a variety of taxa, including captive and natural populations. We selected only studies that included a raw table of dominance contests, although the criteria for outcome varied (e.g., direct aggression and subordination signals). All the datasets in this study included group sizes of at least 10 animals, to facilitate certain analyses that become problematic for very small numbers of animals. Further, we restricted our choice to datasets that were not tournaments. In a tournament, every dyad has a relation (no null dyads, or double-zeros in the data matrix). Tournaments are very rare in nature, except in experimental, captive situations for relatively small groups, where the possibility exists that interactions cannot be avoided, even if one or other of the interactors would have been an avoider in nature. Because tournaments may be subject to unnatural circumstances, such as forced contests that either or both contestants might avoid in nature, they may produce artifacts such as desperado effects (Grafen 1987) that we felt might obscure the fundamental structural dynamics of the networks.

### Contest matrix, outcome matrix, adjacency matrix, triad census, and network metrics

All input data were contest matrices found as tables or figures in the 40 published studies. From each weighted, directed *contest matrix* we computed an unweighted, directed 1/0 *outcome matrix*, using the majority-win and draw-elimination criteria described in the next paragraph. The contest and outcome matrices are directly equivalent to adjacency matrices (Newman 2003), one of the most widely used forms of input for network analyses. In the resulting networks, the *nodes* are individual animals and the *edges* are either numbers of contests won or lost (contest matrix) or 1/0 dominance relations (outcome matrix).

Unresolved contest sets (draws, in which each contestant wins an equal number of contests) present a potential source of uncertainty and concern for analysis of dominance hierarchies. For example, in assigning outcomes, draws could be designated by a 0 for each participant (Chase 1980), or by a score of 0.5 for each (Appleby 1983). We will use the former convention, whereby draws result in a 0 for each contestant. We justify eliminating draws for 3 reasons. 1) It

simplifies the network perspective, by yielding a network with only asymmetric edges (1-way arrows from a clear dominant to the clear subordinate) and no mutual edges (Holland and Leinhardt 1976). 2) Ignoring draws leads to a simpler triad census (Figure 1), a social network technique (Holland and Leinhardt 1976) that we use to quantify the distribution of triadic configurations (Chase 1982; Faust 2010) in the dominance datasets. We were particularly interested in those triad types, such as *Cycles* (Figure 1) that pertain directly to the orderliness of the social structure. The triad census for a network with mutual edges has 16 types; if draws (mutual edges) are ignored only 7 easily interpreted types exist (Figure 1). 3) Draws were rare and, as discussed below, we tested the robustness of our conclusions by conducting analyses in which draws were not ignored. Of our 40 datasets, 15 had no draws at all. Of the 25 datasets that did have draws, fewer than 2% of the dyads had sets of contests resulting in draws, and they accounted for just 1.3% of the total number of contests. When dyads did engage in bouts of contests that resulted in draws, the mean number of contests was $1.8 \pm 1.3$, meaning they were rarely protracted, and therefore not greatly different from the 0/0 that would have resulted had no contest occurred. Further, the vast majority of dyadic outcomes that did not result in draws had highly lopsided contest counts.

From each outcome matrix, we computed the triad census using routines in the *Statnet* (Handcock et al. 2003) and *iGraph* (Csárdi and Nepusz 2006) packages of the *R* programming framework (R Development Core Team 2009). Only the 7 triad types shown in Figure 1 are possible for a network that has asymmetric (directed, 1-way) and null (missing) edges but not mutual (directed, 2-way) edges. *R* scripts for all analyses can be found on the senior author's website (http://www.uwyo.edu/dbmcd/mcd.html). The number of triads in a network is a combinatorial (*n-choose-3*) function of the number of nodes, and increases rapidly with node number (group size), $n$ ($n = 4$, 4 triads; $n = 6$, 20; $n = 8$, 56; $n = 10$, 120). Note that triads are not likely to be independent; for example, with individuals labeled alphabetically, several triads could include individual $A$ (e.g., *ACE*, *ADH*, and *AFJ*). Such nonindependence invalidates some traditional statistical tests and requires randomization procedures, such as Mantel tests.

We calculated the network density, $d$, defined as the proportion of possible edges (nonzero outcome-matrix entries) that actually occur. Note that, because of our no-draw simplification, the maximum number of cells that can be filled is one-half the number of nondiagonal cells (i.e., equals the number of cells in the upper diagonal, in a perfectly transitive hierarchy). Thus, if $e$ is the number of directed edges in the network (values of 1 in the outcome matrix), the density of the outcome matrix, $d = e/[0.5 \times n \times (n-1)]$, is twice the conventional metric for other types of networks, such as undirected networks; the difference arises because no mutual edges are allowed. That is, any reversals (a 1 in a lower diagonal cell of the matrix, meaning that a lower ranking animal dominates a higher ranking animal) must be balanced by a 0 in the corresponding cell of the upper diagonal of the 1/0 outcome matrix. We also calculated the global clustering coefficient, which is well described in Newman (2003). From the perspective of an individual (node), the global clustering coefficient can be interpreted as the probability that the 2 neighbors of a given node are themselves each other's neighbors. The higher the clustering coefficient, the more densely interconnected the nodes in the network are. We also calculated *betweenness*, a centrality measure that assesses how often a node lies along the shortest paths between all pairs of nodes in the network, to

ascertain whether individuals involved in *Cycles* also showed high network centrality.

## Calculation of triangle transitivity, $T_{tri}$, for empirical networks

Networks with noninteractions (null dyads) complicate the calculation of "linearity." One of the leading methods for calculating the linearity of a dominance hierarchy (de Vries 1998) requires repeated, imputed (random) fills of null dyads, a requirement that we suggest cause consistent underestimation of the true transitivity (linearity) of animal societies (Shizuka and McDonald 2012). A complete network, with no missing dyadic outcomes, is known as a tournament. For networks, such as our *outcome* networks, with only asymmetric edges, a tournament has only 2 of the 7 types of triads—*Transitives* (Figure 1; *A* dominates B and *C, B* dominates *C*, yielding a clear top, middle, and bottom animal) and *Cycles* (Figure 1; *A* dominates *B*, which dominates *C*, which dominates *A*, yielding no clear top animal). For a tournament, therefore, the transitivity would be simply the proportion of the *Transitive* triangles divided by the sum of the *Transitives* and *Cycles*. Nevertheless, even if incomplete triads occur, a straightforward and relatively assumption-free measure of transitivity is possible (Shizuka and McDonald 2012), using only the proportion of transitive triangles relative to the total of *Transitive* triangles and *Cycles*, scaled relative to the null expectation (from random directed networks; Faust 2007, 2010) of a proportion of 0.75 of transitive triangles. We call this measure the *triangle transitivity, $t_{tri}$*. It is calculated as:

$$t_{tri} = 4\left(\frac{N_{transitive}}{N_{transitive} + N_{cycle}} - 0.75\right) \qquad (1)$$

where $N_{transitive}$ and $N_{cycle}$ refer to the number of *Transitive* triads and *Cycles*, respectively, computed in the triad census (Holland and Leinhardt 1976; Figure 1). The value of $t_{tri}$ usually ranges from 0, when the proportion of transitive triangles equals the random expectation of 0.75, to 1, when only transitive triangles occur. Although the value of $t_{tri}$ can be slightly negative when *Transitive* triangles constitute less than the 0.75 random expected proportion, negative $t_{tri}$ values seem rarely to occur in empirical networks (e.g., 0 of 101 dominance networks in Shizuka and McDonald 2012).

## Generation of random networks and observed minus expected triad census

Random networks have long served as the core "null model" for network analyses (Erdös and Renyi 1960; Wasserman and Faust 1994; Watts and Strogatz 1998). For our purposes, the most important feature of random directed networks is that their expected proportion (from among all triangles—triads with all 3 "legs") of *Transitive* triangles is 0.75, whereas their expected proportion of *Cycles* is 0.25. Our major use of replicate random networks in this article is to generate "expected" frequencies of the 7 distinct (nonisomorphic) triad types shown in Figure 1. *Pass-along* triads can play a pivotal role in the emerging orderliness of a group because, depending on the directionality of the third edge in the event of a contest between the noninteracting dyad, they can become either *Cycles* (disorderly) or *Transitive* (orderly) triads. That is, every *Cycle* has a *Pass-along* as a precursor, but not all *Pass-alongs* will become *Cycles*. Thus, if for example, a dataset has a paucity of *Pass-alongs*, one can infer that *Cycles* might also show a deficit in those 2-edge triads for which the third edge forms. The other 2 two-edge triad types, *Double-dominant* and *Double-subordinate*, are necessarily

orderly. No matter which way the third edge points they will become *Transitive* triangles.

We used *R* scripts to analyze the empirical dominance datasets and to generate 10 000 replicate random networks corresponding to each empirical network. We constrained the 10 000 random directed networks to have the same number of nodes (animals) and edges (dominance relations) as the comparator empirical network. In network parlance, such networks are known as dyad census-conditioned uniform random graphs, which we generated using StatNet's (Handcock et al. 1993) *rguman* function in *R*. For each random replicate, we calculated the difference between the (expected) percentage of a particular triad type in the random (null model) graph replicate and the (observed) percentage of the given triad type in the empirical, published dominance dataset. We then plotted the mean observed versus expected difference with a 95% confidence interval derived from the 2.5 to 97.5 percentiles of the 10 000 observed minus expected difference values. Any observed versus expected confidence intervals that do not overlap 0 are therefore significantly positive at the 5% level (i.e., showing an excess of that triad type in the empirical network compared with the random, null expectation) or negative (deficit of that type of triad in the empirical network).

## Assessing the effect of outcome uncertainty

The number of contests that determines the 1/0 dominance relation varies among dyads within a dataset and across datasets. A contest set in which 1 animal wins 23 contests and the other wins 1 is clearly a much more certain outcome than a contest set in which 1 wins 23 contests and the other 22. We assessed the effect of this form of uncertainty by reversing the 1/0 outcomes for all contest sets that were close (the number of wins differed only by 1). Further, rather than simply ignoring draws (giving them a 0/0 outcome), we randomly assigned a dominance outcome to dyads whose contest sets resulted in a nonzero draw. Note that such a random assignment should favor the emergence of disorder, because random graphs have an expectation of 25% cycles, an expectation virtually never observed in published datasets (Shizuka and McDonald 2012). We used these rules to reassess the orderliness of the 8 datasets with the highest proportion of close and drawn contest sets.

## Static versus dynamic calculation of rank order

Many analyses of dominance relations do not require assigning ranks. For example, triad census analyses and centrality measures do not depend on assignment of rank, although rank may often be useful as a node or individual attribute, just as one might use gender or age as an attribute. Optimal rank ordering can depend on, among other factors, whether the data are 1) static (fixed at a single point in time), represented by a "final" result, such as that found in many published studies, or 2) dynamic, where the entire sequence of dyadic contests and their outcomes is available, which is rarely the case in published studies. Although multiple alternative ranking methods exist (Hemelrijk et al. 2005; Whitehead 2008), most were highly correlated for our datasets. We used the well-justified method of de Vries (1998) for "static" rankings calculated from the summary contest matrices. The goal of de Vries's method is to arrange the rows and columns to be, as much as possible, in the upper triangular of the matrix, similar to the upper triangularization bandwidth problem in linear algebra (Axler 1996). A perfectly linear hierarchy would have no nonzero cells below the diagonal. Recently,

Neumann et al. (2011; see also Albers and de Vries 2001) proposed the dynamic, updatable Elo-rating method, developed for rating chess players (Elo 1978), as useful for the context of dominance. The method proceeds by starting all contestants with the same initial score (e.g., 1000, as implemented here) and then having an increment/decrement for the winner and loser of each contest (e.g., 100, as implemented here). Scores are interpolated across the intervals in which group members do not engage in contests. The result is a set of scores, dynamically updated after each contest, from which ranks can be assigned. Elo rating has the advantage of dealing very well with "missing" data (null dyads that do not interact), can be implemented (dynamically) from the simple sequence of dyadic contests, and can be readily assessed for temporal stability (Neumann et al. 2011), using a method that we modify to range from 0 (unstable) to 1 (stable), as described below.

### Simulation of contest trajectories, rank stability, and hierarchy steepness

The datasets we analyzed were "static" endpoint tables, summarizing contest data. They did not, therefore, provide the detailed sequence of contest outcomes required for Elo-rating analysis. The numbers in the contest matrices represented the set of all observed dyadic contests in the original data, but did not contain any information on the actual sequence in which the contests occurred. Because we did not have the raw data with which to generate the actual sequences, we generated a set of 200 replicate putative sequences for each of the 40 datasets, by randomly selecting and "backdropping" observed contests. Backdropping consisted of randomly removing contests, one by one, with uniform probability, until only a single contest remained, while keeping a (backwards) list of the sequence of contests. Each random removal generated a winner–loser dyad, resulting in a (backward) sequence of dyadic contests. Once the backwards list was reversed, we had an estimated time-ordered sequence of contest outcomes for a more dynamic exploration of the ontogeny of the hierarchy. That is, each sequence had winners in 1 column and losers in the other, with the number of rows equaling the sum of all the numbers, $\Sigma C_{ij}$, where the $C_{ij}$ are the matrix elements in the original contest matrix with $i$ rows and $j = i$ columns. Note that, because we dropped observed contests, no imputation of outcome was required (only of their temporal order). The total number of contests in the datasets (sum of all the numbers in the contest matrix) ranged from as few as 44 to as many as 2231, meaning that some simulations were computation intensive. We repeated the randomized backdropping across 200 runs for each dataset. The 200 putative sequences (each of the 200 replicates ranged in length from 44 contests to 2231 across the 40 datasets), then served as input to create Elo-rating trajectories—a sequence of Elo scores that we used to generate rank orderings that could be dynamically updated, contest by contest. Analyses for each Elo-rating simulation (examples presented in Figure 4) were computation intensive, taking up to several hours to run a single contest trajectory (on a 2.2 GHz Intel Core i7 MacBook™). We checked the robustness of the random backdropping procedure in 2 ways: 1) we calculated the standard deviation (SD) of the estimate across the 200 replicates, and by comparing the mean and median to check for skewed distributions. A small SD would mean that any of the replicate runs is a reasonable representative of the process, and suggest that the actual sequence was unlikely to have differed greatly from the sequence obtained by the simulated backdrop

procedure. A small difference between mean and median would mean that the distribution of estimates across the runs did not have a long tail, reducing the possibility that the actual (unpublished) sequence differed from most of the simulated backdrop replicates. 2) We compared the outcome of our random backdropping estimate of the rank stability index with that calculated from the actual temporally ordered data for a study (Wittemyer and Getz 2007) whose raw data the authors made available to us.

The stability of rank orders across time (measured as sequential contests) is one of the factors we considered in assessing the orderliness of the 40 dominance hierarchies. For each of the 200 simulated trajectories, we computed a stability index that assesses how frequently rank switches occur. The stability index proposed by Neumann et al. (2011) has 2 unfortunate attributes: an upper bound that varies with group size, and a range from a counterintuitive "most stable" = 0 to "less stable" for higher values that depend on group size. We therefore modified the Neumann stability index to range from 0 (completely unstable) to 1 (most stable), independent of group size. Our modified stability index is

$$St = 1 - \frac{S}{2n} \qquad (2)$$

where $n$ is the number of animals in the group, and $S$ is Neumann et al.'s (2011) stability index (their Equation 5). Note that their stated maximum for $S$ is a typographical error that should be $2 \times n$ not $2/n$ as typeset because maximal instability occurs for the summed absolute differences of completely reversed rank orders. For comparing stability (described above; Equation 2) across the datasets, we calculated the mean value across the 200 runs, and used the simulation closest to the mean when producing figures representing rank-score trajectories for that dataset. We checked both the mean-median difference of the stability index and the SD across the 200 runs to check whether any particular simulated run was likely to be representative of the actual (unpublished) sequence of contests.

For the representative (mean) trajectory, we also computed the steepness of the final Elo-rating ranking (i.e., we computed the Elo ratings, and thereby the rank order, at the point where all the backdropped contests had been restored to the contest matrix). Because the distribution of Elo-rating scores within a hierarchy is often decidedly skewed, we used the Gini coefficient as an index of steepness, rather than the slope of linearly regressing rank against score that was proposed by de Vries et al. (2006). The Gini coefficient is often used, in other contexts, as a measure of inequality derived from the Lorenz curve (Weiner and Solbrig 1984; Wittebole et al. 2009). The Gini coefficient is given by:

$$G = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{2n^2 \mu} \qquad (3)$$

where the $x_i$ are the Elo scores for the $n$ individuals in the group, and $\mu$ is the mean score (Equation 2 in Damgaard and Weiner 2000). Because it is a single-number summary, the Gini coefficient does not contain all the information about the curve. That is, 2 differently shaped curves can have the same Gini coefficient. As a supplement to the Gini coefficient, Damgaard and Weiner (2000), therefore, proposed also assessing the *Lorenz asymmetry coefficient*, whose value is <1 if the bulge of the curve lies below an imaginary line of slope −1, and >1 if the bulge lies above the imaginary line of slope −1. Values of the coefficient <1 can be interpreted to mean that the main source of inequality arises from individuals with low scores (low-ranked individuals), whereas values >1 mean

inequality attributable to top-ranking individuals. As the basis for significance testing, on each of 1000 iterations we first randomly reassigned winner and loser status in the $\Sigma C_{ij}$ rows of the contest sequence set produced by the backdropping technique described above. We then calculated the Gini coefficient for the randomly adjusted sequence set. Finally, we assessed the significance of the observed Gini coefficient by its placement in the set of 1000 randomized Gini coefficients. As a further measure of the source of the inequality, we computed the Gini coefficient for just the 4 top-ranked individuals in the hierarchy. A high value of this "top 4" Gini coefficient would mean that the scores dropped off sharply even among the top-ranked individuals. Because benefits, but perhaps sometimes costs (Gesquiere et al. 2011) likely accrue most importantly to top-ranked individuals, pinpointing the location of the "bulge" in the Lorenz curve should be useful when comparing the steepness characteristics of different datasets, or the same dataset over time.

## RESULTS

The 40 datasets had a mean of 16.3 nodes (range 10–38, SD= 6.2) and 87.7 edges (range 19–409, SD = 77.6) in the 1/0 outcome matrix, derived from the raw contest matrices presented in the source articles. The datasets were sparse, containing many noninteracting dyads, yielding a mean density of 0.66 (proportion of all possible edges that actually occurred; Appendix 2), with most of the high values occurring in captive or experimental situations. The total number of contests in the contest matrix averaged 559.6 (range 44–2231). Draws were rare, averaging 1.8% of the dyadic contest sets, with no draws at all occurring in 15 of the 40 datasets. Draws tended to occur between animals closer in rank than expected. The mean rank difference between animals whose contest bouts resulted in a draw was 3.1 versus an expected mean rank difference of 6.3. Figure 2 shows dominance-related metrics whose possible values fall in the interval from 0 to 1. The triangle transitivity index, $t_{tri}$, varied from a low value of 0.37 to a maximum of 1.0 ($\bar{x}$ = 0.88, SD = 0.16). In 33 of the 40 datasets, none of the 10 000 random network $t_{tri}$ overlapped with the observed $t_{tri}$ value ($P < 0.0001$). Only 1 dataset (Natoli and DeVito 1991), for feral cats *Felis sylvestris catus*, had a nonsignificant ($P = 0.27$) difference between the observed and random $t_{tri}$ (Appendix 2). Nine of the 40 datasets were for birds, 9 were for primates, 18 were for nonprimate mammals, 2 were for fish, and 2 for invertebrates. For none of the metrics presented in Figure 2
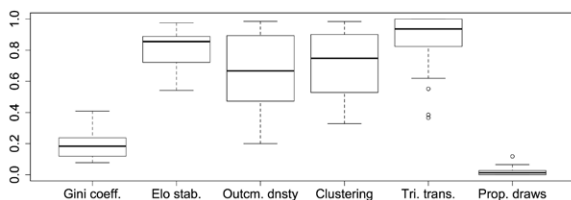


**Figure 2**
Box-and-whisker plots for various metrics for the 40 datasets. The heavy horizontal line denotes the median. The box spans the 25–75th percentiles of the data. The vertical dashed lines encompass either the range of the data, or, if outliers exist (open circles), 1.5 times the interquartile range of the data. 1) Gini coefficient of inequality (a measure of the steepness of the rank scores using Elo rating); 2) Elo-rating rank stability index; 3) density of the outcome matrix; 4) global clustering coefficient; 5) triangle transitivity, $t_{tri}$, the expected $t_{tri}$ in a random network is 0; 6) proportion of dyads whose contest bouts resulted in draws.

was there any clear pattern of difference among these broad taxon groups (Appendix 2).

Although the pattern of triad distributions for the triad census (Figure 3 and Appendix 3) varied across the 40 datasets, a typical pattern was to have a significant excess of *Double-dominant* (27 of 40), and *Transitive* triads (38 of 40), and a significant deficit of *Pass-along* (true of 35 of 40) and *Cycle* triads (38 of 40). The deficit of *Cycles* was even more pronounced than the deficit of *Pass-alongs* for the majority (22 of 40) of datasets, meaning that the mean observed minus expected percentage was more negative, and the upper end of the 95% confidence interval further from the zero line for *Cycles* than for *Pass-alongs* (Figure 3). Thirteen of the 40 datasets had no *Cycles* at all (Appendix 2); on average, *Cycles* represented only 1.0% of the total triads in the datasets. Only 1 dataset (Poisbleau et al. 2006, Figure 2a; 8.4%) had >5% *Cycles*. Only 1 dataset (Nakano 1994; red-spotted masu salmon; Figure 3, middle) had a mean observed minus expected difference for *Pass-alongs* that was positive, although its 95% CI overlapped zero.

Outcome uncertainty did not affect the conclusion that dominance structures are orderly. Uncertainty about the dominant-subordinate relation is highest for contest sets resulting in nonzero draws and close sets (wins differing from losses by a single contest). Draws were rare (mean proportion < 0.02; Appendix 2) and close contests never exceeded 6% of the total contests. None of the 8 datasets with the highest number of close contest sets and draws (highlighted by an asterisk next to the taxon name in Appendix 2) showed any change in the distribution of observed versus expected outcomes for the triad census under the uncertainty reversal routine. That is, in all cases, regardless of the reversal of 1/0 dominance outcomes, the datasets showed the same pattern of significant excess of *Double-dominant* and *Transitive* triads, and a deficit of *Pass-along* and *Cycle* triads.

The trajectories of rank orderings (Figure 4), evaluated by Elo rating (Neumann et al. 2011), varied across the 40 datasets, with a mean stability index of 0.81 (SD = 0.13, range 0.54–0.98; Appendix 2). A stability index value near 1 means that the rank orders (determined by continually updated Elo scores) rarely changed, as shown by a fairly typical paucity of line crossing in Figure 4B. Lower values of the stability index indicate more frequent rank order changes, as shown by frequent line crossings for one of the least stable dominance rank orders in Figure 4A. Within each of the 40 datasets, the stability index estimate varied little across the 200 replicate backdropped runs (mean SD = 0.02) and all means and medians were very similar, meaning that any of the replicate backdropped contest sequences was reasonably representative of all the other runs. Further, for the 1 dataset (Wittemyer and Getz 2007) for which we were able to compute the stability index from the actual raw data, the actual (0.586) and estimated (0.557) values were very similar. The stability index was highly correlated with the Gini coefficient, a measure of the steepness of the ranking scores (Figure 5; $R^2_{adj}$ = 0.67, F = 80.03, df = 38, $P < 0.0001$). The Gini coefficients for the 40 datasets ranged from 0.08 to 0.41 ($\bar{x}$ = 0.18, SD = 0.07; Appendix 2).

By measuring the asymmetry of Lorenz curves for the Elo-rating rank scores, one can determine whether the steepness of rank-score differences are driven mainly by inequalities among the top-ranked or the bottom-ranked individuals (see Methods; Damgaard and Weiner 2000). For the 40 datasets, the Lorenz asymmetry coefficient (Figure 6) ranged from 0.75 (meaning that the inequalities occurred mostly in the top half of the hierarchy) to 1.42 (meaning that the inequalities occurred mainly in the bottom half of the hierarchy). About half the datasets (22) had asymmetry coefficients <1. The mean Lorenz asymmetry coefficient across all 40
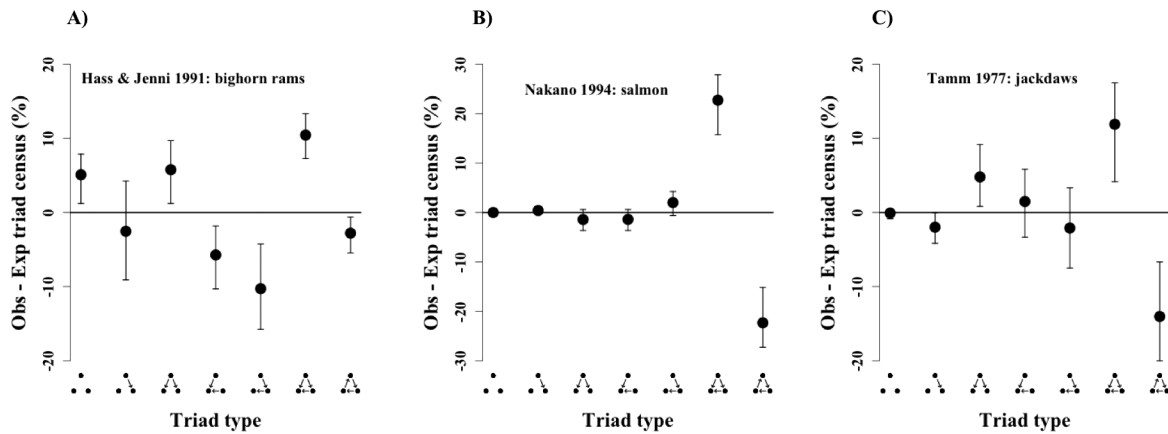
**Figure 3**
Difference (mean and 95% CI) between the observed (empirical data) and expected (random) triad percentage from the triad census for 3 of the 40 dominance datasets. The *y* axis is the percentage (among *n-choose-3* observed triads in the data) of the 7 triad types, minus the mean triad census percentage from 1000 random networks (+95% CI). Thus, *y* axis values are the difference between observed and expected percentage for the 7 possible triad types depicted by the diagrams along the *x* axis (see Figure 1). Using pecentage allows comparison across networks of different size. A) *Ovis canadensis* data, with a "typical" excess of *Double-dominant* and *Transitive* triads, and a deficit of *Pass-along* and *Cycle* triads. B) A less typical near-tournament in salmon data, consisting almost exclusively of *Transitive* and *Cycle* triangles. C) Another "less typical" pattern for *Corvus monedula*, whose 95% confidence interval for *Pass-alongs* extended well across both sides of the zero line, although the mean was still a deficit. All 3 datasets had a significant excess of *Transitives* and a significant deficit of *Cycles*. As was true for virtually all of the 40 datasets, therefore, the hierarchies were more orderly than expected by chance.

datasets was 1.0, the value associated with a symmetric curve. Because the most important rank score differences should be those involving the top-ranked individuals, we also assessed the Gini coefficient for just the 4 top-ranked individuals in each dataset, which was weakly but significantly correlated with the Lorenz asymmetry coefficient ($R^2_{adj} = 0.08$, $F = 4.3$, df = 38, $P < 0.05$). Despite the range of values for the Gini and Lorenz asymmetry coefficients, all 40 datasets had observed Gini coefficients that were significantly ($P < 0.001$) higher than the expected (randomized sequence sets) values, meaning that they were all "steep," despite varying in degree of steepness and in where the steepest part of the drop in scores occurred.

In the 27 dominance networks with 1 or more triadic *Cycles* (Appendix 2), certain individuals tended to be overrepresented as participants in these disorder-inducing interactions. For example, in the data for female African elephants, *Loxodonta africana*, of Wittemyer and Getz (2007), female *R37* (13th in the rank order) was involved in the only 2 *Cycles*, which otherwise had no overlapping members. In 1 *Cycle*, she dominated the female 5 ranks above her, whereas in the other *Cycle* she was dominated by a female 2 ranks below her. Interestingly, elephant *R37* was both old (usually positively correlated with high rank) and small (usually negatively correlated with high rank; Wittemyer G, personal communication). Although this level of individual detail was not available for most of the other
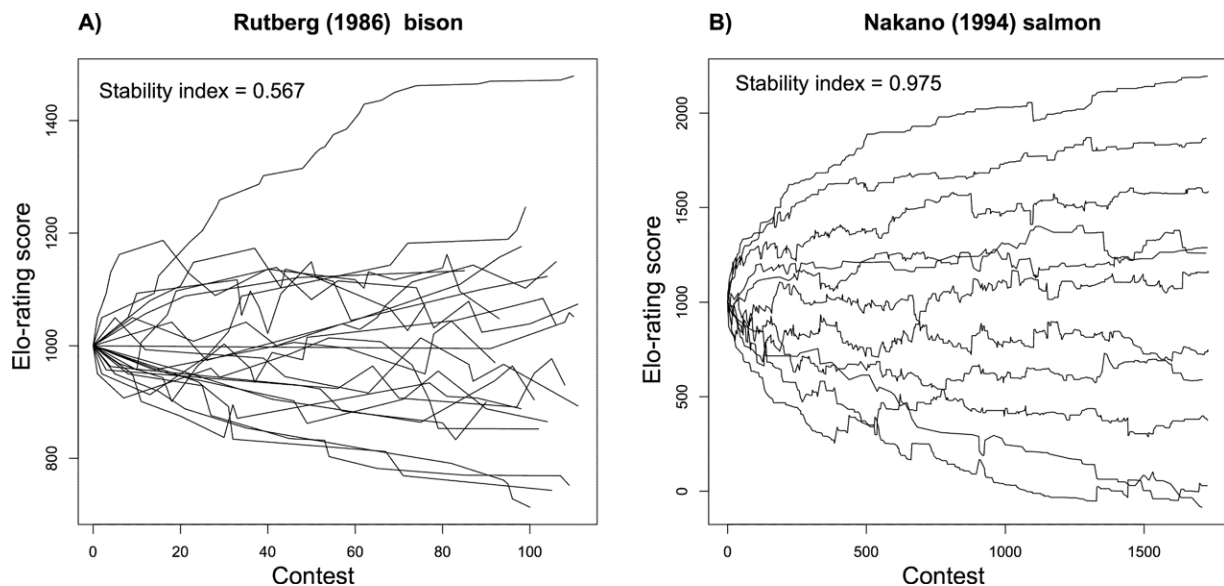


**Figure 4**
Trajectory of Elo-rating scores (*y* axis) over a series of contests (*x* axis). A) Female American bison (*Bison bison*) had a rather low stability index of 0.57 (many rank changes) during the course of their 112 dyadic contests, although note the early and clear gap between the top-ranked individual and all the rest. B) Red-spotted masu salmon (*Oncorhynchus masou ishikawai*) data had a high stability index of 0.98 during the course of their series of 1732 dyadic contests.
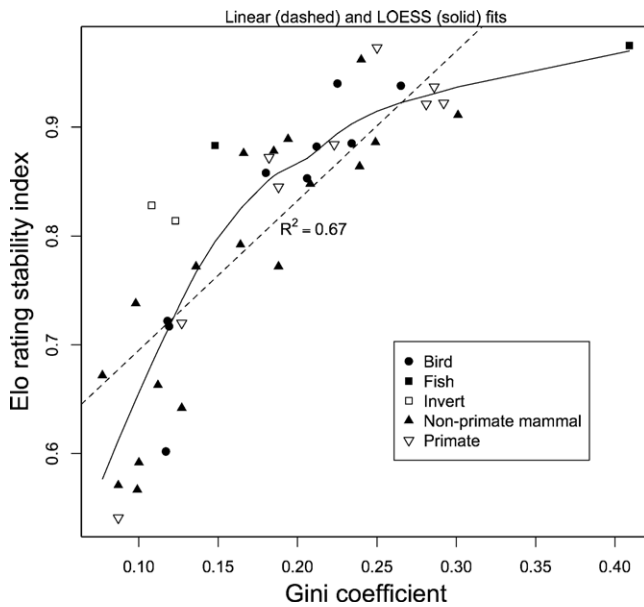
**Figure 5**

Relationship between the stability index for Elo-rating ranks and the Gini coefficient for the 40 dominance datasets. The Gini coefficient (derived from the Lorenz curve; range 0.08–0.41; Appendix 2) is a measure of inequality, and is larger for rankings with high disparity in Elo-rating scores of individuals in the hierarchy. The 0–1.0 stability index (Appendix 2), modified from Neumann et al. (2011), describes the frequency of rank order changes in a sequence of contests such as those depicted in Figure 4. Not surprisingly, steep hierarchies with steep differences in Elo-rating rank scores, as assessed by the Gini coefficient, also tended to show high stability of rank order.

datasets, patterns of individual involvement in *Cycles* had a few consistent patterns in the 40 datasets. For the 5 datasets with the largest number of *Cycles* (Appendix 2), those individuals most heavily involved in *Cycles* were generally mid-ranking animals (mean normalized rank = 0.47 on a scale of 0–1). One standard network metric of centrality, *betweenness,* was not well correlated with involvement in *Cycles* ($R^2 = 0.02$, $P > 0.05$). Although individuals heavily involved in *Cycles* tended to have high betweenness, in no case did the individual with the highest betweenness also participate in the greatest number of *Cycles*.

## DISCUSSION

The overwhelming picture that emerges from our examination of the 40 datasets is that most are highly orderly, whether viewed through the lens of triangle transitivity, $t_{tri,}$ or from the perspective of the temporal Elo-rating stability ($\bar{St} = 0.81$ on a scale from 0 to 1). Further, all 40 datasets had Gini coefficients (steepness measures) significantly greater than the random expectation. A steep hierarchy means that the differences between ranks are greater, and therefore that the odds of rank changes, especially among individuals of non-adjacent rank, are less likely to occur. The results of the triad census analyses (Appendix 3) also reinforce the conclusion of general orderliness, with their significant excesses of *Double-dominant* (27 of 40 datasets) and *Transitive* (38 of 40) triads, and their significant deficits of *Pass-along* (35 of 40) and *Cycle* (38 of 40) triads. Note that, regardless of the eventual dominant in the "missing" edge of a *Double-dominant* triad, the only possible "filled" 3-edge triangle is a *Transitive*. After a contest between the dyad in the "missing leg" of a *Pass-along*, it can become either a *Transitive* or a *Cycle*, depending on the direction of the edge that completes the triangle. Because the deficit of *Cycles* was even more pronounced than the deficit of *Pass-alongs* for the majority (22 of 40) of datasets (Appendix 3), the data suggested that a higher than expected proportion of previous *Pass-alongs* converted to *Transitives*, and a lower proportion than expected became *Cycles*. Thus, the finding that the "typical pattern" (Appendix 3) includes an
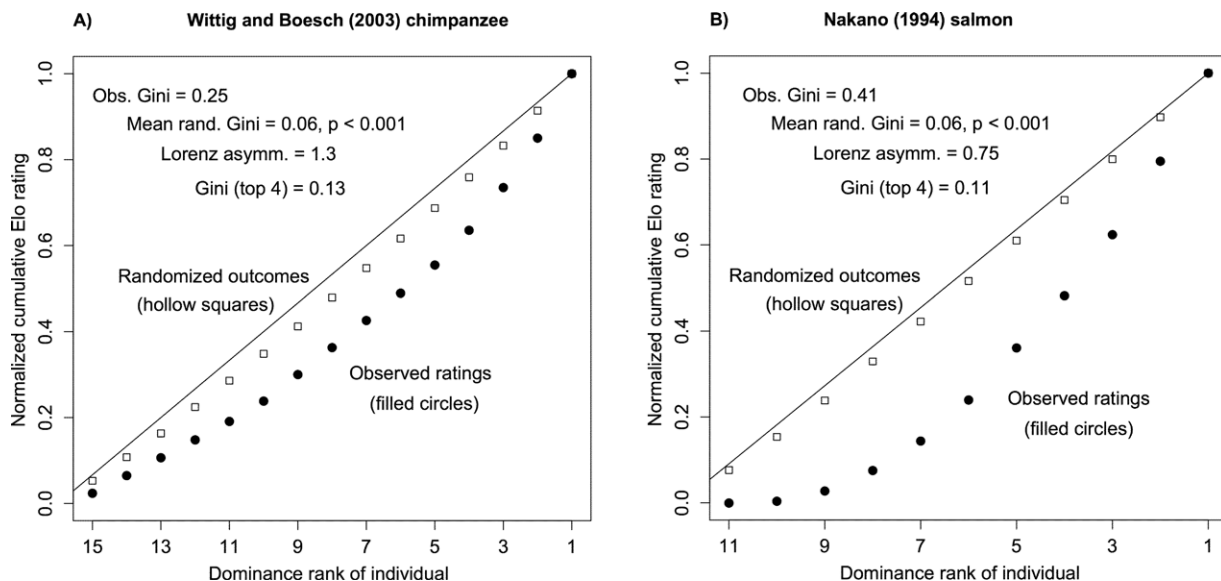


**Figure 6**

Lorenz curves for 2 representative datasets, with rank from lowest (*n*) to highest (1) on the *x* axis and normalized, cumulative final Elo-rating score on the *y* axis. The shape informs as to whether rank inequality occurred mostly among animals in the top (Lorenz asymmetry coefficient > 1) or bottom (Lorenz asymmetry coefficient < 1) half of the hierarchy respectively. A) For female chimpanzees, the rank inequality was less steep, but the bulk of the inequality came from high-ranked animals (bulge of the curve lies above an imaginary line of slope −1), as assessed by the Lorenz asymmetry coefficient (1.3). Also shown is the Gini coefficient (0.13) for the 4 top-ranked individuals, which is higher (steeper) than for the 4 top-ranked fish in B. B) For red-spotted masu salmon, the ranks dropped steeply, but the bulk of the inequality arose from the very low scores of the lowest-ranking animals (bulge of the curve lies below the imaginary line of slope −1), as assessed by the Lorenz coefficient (0.75). The Gini coefficient of the 4 top-ranked individuals (0.11) was less than that for the chimpanzee data.

excess of *Double-dominant* triads and a deficit of *Pass-along* triads reinforces the 40-dataset pattern of orderliness suggested by the triangle transitivity index, $t_{\text{tri}}$ (Appendix 2), which considers only the proportions of *Transitive* and *Cycle* triads. We can confidently conclude that, for the sample of dominance hierarchies examined here, triadic relations are more transitive than expected by chance, and that the hierarchies tend to be fairly steep and temporally stable (mean rank stability index of 0.81 on a scale of 0–1). To paraphrase Orwell (1945), all dominance hierarchies are orderly, even if some are more orderly than others. Furthermore, outcome uncertainty arising from ignoring draws and from deeming individuals as dominant even if they won a contest set by a very narrow margin, such as 23 to 22, had no effect on the conclusion of orderliness. Obviously, being dominant or subordinate might have major effects on all aspects of the lives of the individuals involved, but outcome uncertainty does not result in any higher order change in the fundamental orderliness of the group or society.

The excess of *Null* triads in some of the datasets (significant excess in 13 of 40, trend in an additional 12; Appendix 3), and the rather low mean density ($\bar{d} = 0.67$; Figure 2) of the 40 outcome matrices, is consistent with the notion that empirical datasets are often sparse. Many dyads never interact. Because many of these datasets were from intensive, long-term studies, it seems unlikely that the prevalence of null dyads can be explained away as merely a consequence of insufficient sampling or the low interactivity of a few individuals. Instead, they support the hypothesis of active avoidance driven by bystander effects, whereby observing the interactions of others influences an actor's subsequent interaction probability (Oliveira et al. 1998). Such nonrandom patterns of avoidance likely contribute to the striking scarcity of cyclic triads in dominance hierarchies, and to the near-universal observation that, even after long observation of natural groups of animals, many null dyads persist. That is, despite abundant opportunity, many dominance interactions fail to occur.

Viewing dominance data at a range of scales from dyadic to triadic and at the level of the group as a whole can enrich our understanding of process and can help to suggest hypotheses subject to observational and experimental test. Although dyadic interactions may largely determine higher level network properties (Faust 2007), examining triadic patterns (Broom et al. 2009; Faust 2010) is worthwhile, as demonstrated by the results from the triad census analyses. The broad "typical" pattern (Figure 3) of a significant excess of *Double-dominant* and *Transitive* triads, and a significant deficit of *Pass-along* and *Cycle* triads, suggests that disparate taxa and functionally different social groupings may tend to share certain common features whereby orderly groupings provide at least some benefits, of various sorts (e.g., reduced time spent in agonistic encounters), to all group members (Flack et al. 2006). Chase (1982) pointed out that *Pass-alongs* could form in 1 of 2 ways. If the 3 members of the triad are designated *A*, *B*, and *C* and the *Pass-along* consists of *A* dominating *B* and *B* dominating *C*, either the *A–B* leg or the *B–C* leg could arise first. The sequence of contests is an important component of the outcome in dominance relations. For example, if *Pass-alongs* generally arise because *A* dominates *B* followed by *B* dominating *C*, that result weakens support for the loser effect hypothesis, whereby losers become entrained to lose or to avoid contests. Unfortunately, most published data are "static" summaries of cumulative dominance contests, and the detailed time ordering of contests, an inevitable feature of the raw data, is rarely presented in the published study. In this study, we have attempted to analyze the dynamic stability of dominance relations using a random backdrop

procedure. Careful consideration of the temporal dynamics of dominance relations from the raw data, using methods such as R codes to calculate the stability index, could produce many more insights into the processes that lead to order in animal societies. Such studies could illuminate the role of early contest outcomes, third-party observer effects on dominance dynamics, and the plausibility of winner or loser effects, and help to assess whether avoidance is an important factor in creating the sparseness of dominance matrices.

Primates are sometimes considered as an exception to rules governing dominance interactions, because of their tendency to engage in coalitions and "dependent dominance" (Jolly 1972; Chase 1980), whereby an animal's dominance rank can dependent on that of its kin or associates. Similarly, maternal rank inheritance in spotted hyenas (Dloniak et al. 2006) complicates any attempt to develop universal rules for establishment of dominance hierarchies and their orderliness. Such complications might seem to be restricted to primates and the complex societies of some carnivores and cetaceans. Nevertheless, coalitions as durable, and perhaps more striking (McDonald and Potts 1994; McDonald 2010) occur in birds. The results of this meta-analysis failed to find any dramatic differences between primates and other taxon groups (compare values for the various network metrics found in Appendix 2). Our goal, however, was not to compare metrics across taxa, but to propose a framework for assessing dominance structures and to use that framework to assess the generality of orderliness in animal societies characterized by dominance interactions. Our findings suggest that fundamental properties of transitivity, hierarchy steepness and rank stability either do not require complex social cognition, or that biologists may have tended to underestimate the social cognitive abilities of other taxa. Furthermore, this general orderliness raises the interesting prospect of a certain degree of self-organization in animal societies, whereby benefits to orderliness exist even for lower ranking animals, despite Maynard Smith's (1983) conjecture that low-ranking animals might almost never having anything to lose from disrupting orderly queues.

## SUPPLEMENTARY MATERIAL

Supplementary material Appendix 1–3 can be found at http://www.beheco.oxfordjournals.org/

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