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A Social Network Perspective on Measurements of Dominance Hierarchies

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Abstract

The hierarchical organization of dominance relations among animals has wide-ranging implications in social evolution. The structure of dominance relations has often been measured using indices of linearity (e.g. Landau's h , Kendall's K): the degree to which dominance relations adhere to a linear hierarchy. An alternative measure is the transitivity of dominance relations among sets of three players that all interact with each other, a measure we call triangle transitivity (t_{tri}). Triangle transitivity and linearity are essentially equivalent when dominance relations of all dyads are known, but such complete observations are rare in empirical studies. Triangle transitivity has two major advantages: it does not require 'filling in' of unobserved relations, and its expected value is constant across group sizes. We use a social network perspective to demonstrate a property of transitivity in random directed networks (on average, three-fourths of complete triads are transitive) and show that empirical dominance networks are often significantly more transitive than random networks. Using 101 published dominance matrices we show that published algorithms for assessing linearity underestimate the level of social orderliness, particularly in larger groups, which tend to have more null dyads. Thus, previous puzzlement over the decrease in estimated linearity in larger groups could be due largely to the bias introduced by random filling of null dyads. We argue that triangle transitivity will allow researchers to focus on important processes underlying the dynamics of dominance, such as spatial segregation, avoidance of interactions by certain individuals and detailed temporal patterns in the ontogeny of hierarchy formation.

Keywords: aggression, imputation, Landau's h , orderliness, peck order, random network, social structure, triad census

The existence of hierarchical order in social systems is a general and striking pattern in nature (Dawkins 1976). A primary example is the prevalence of dominance hierarchies, in which the members of a group establish dominance ranks that influence access to resources or mating opportunities (Drews 1993). How social order on the scale of whole societies or groups can emerge from a series of social interactions between two individuals has been a central question in social biology (Landau, 1951a, 1951b; Chase, 1982a; Dugatkin, 1997; Faust, 2007). An important component of such research is to establish useful metrics that can capture essential aspects of hierarchical organization.

Since the first descriptions of 'peck order' in groups of hens (Schjelderup-Ebbe 1922), studies of dominance structure have often focused on why animal groups often seem to be arranged into linear hierarchies. A strictly linear hierarchy is one in which higher-ranked individuals dominate all individuals of lower rank. Within a strictly linear hierarchy, all dyads have a dominant-subordinate relation, and dominance relations for every set of three players (triads) are 'transitive': when individual A dominates B and B dominates C, then A also dominates C (Chase, 1982a; de Vries, 1995). In contrast, a triad arranged in a 'cycle' (e.g. A dominates B, B dominates C, and C dominates A) results in dominance relations that are unre-

solved and prevents the linear arrangement of ranks. The orderly and predictable arrangement of dominance ranks in a linear hierarchy is thought to have important consequences for individual fitness and group stability (Ellis, 1995; van Doorn et al., 2003; Cant et al., 2006). The structure of dominance hierarchies is typically measured using one of two independently derived indices, Kendall's K and Landau's h (Kendall and Babington Smith, 1940; Landau, 1951a; Appleby, 1983; de Vries, 1995; also see Methods). Although they are not identical, the two indices generally yield the same values (see Methods; de Vries 1995) describing the degree to which an animal group adheres to a strict linear hierarchy. Thus, these indices are commonly referred to as metrics of 'linearity'.

A major limitation of linearity indices is that they become biased when some pairs of individuals fail to interact (de Vries, 1995; Klass and Cords, 2011). This bias arises in part because strict linear hierarchies can occur only in groups where dominant-subordinate relations exist for every dyad in the group. Networks in which all dyadic relations are asymmetrical (e.g. dominant-subordinate) are called 'tournaments' (Harary & Moser 1966). However, tournaments rarely arise naturally in animal groups, and as we will show, unknown dyadic relationships are common because certain pairs of individuals fail to interact (hereafter 'null dyads'). Currently popular

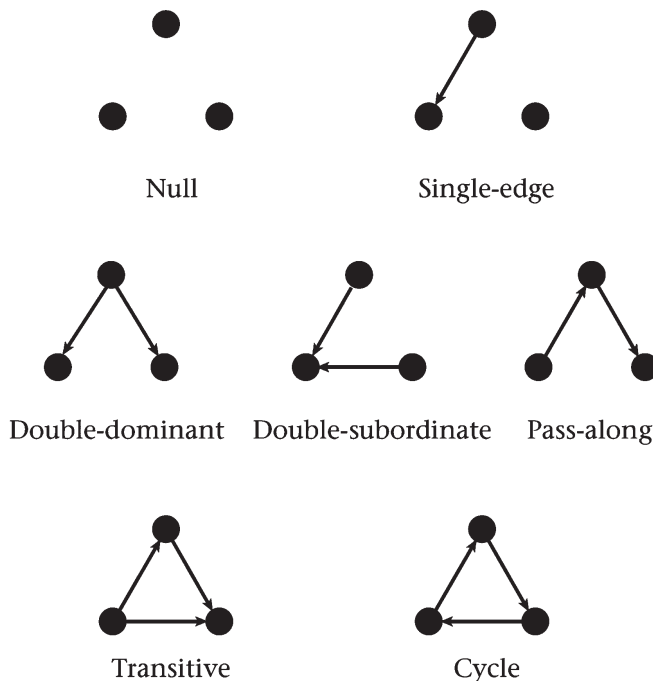


Figure 1. Configurations of seven possible triads in a network with no mutual dyads. Triangles (triads with three edges) can either be 'Transitive' or 'Cyclic'.

methods call for random 'imputation': null dyads (missing data) are 'filled in' with randomized dominance relations (de Vries 1995). Randomization procedures are often used to reduce bias in such imputation methods (Nakagawa & Freckleton 2008). However, we show that random filling of null dyads inevitably produces a different but pernicious negative bias in estimated linearity.

Dyads may fail to interact for multiple reasons, and the processes that lead to noninteractions may be of biological interest. First, spatial or temporal segregation may make it impossible for some dyads to interact. Inferring a dominance relation between such individuals would be a purely artificial exercise. Alternatively, some individuals may actively avoid interactions. Such avoidance could arise because the costs of interaction are too high (e.g. escalation of contest is likely), the potential benefits of interaction are too low, or because dominance relations can be settled without resorting to overt interactions (e.g. by long-distance signalling or by third-party effects). Finally, some interactions may simply have been unobserved. It is difficult and often impossible to distinguish between these processes that give rise to noninteractions. However, it is possible to measure directly the frequency of transitive and cyclic triadic relations within the observed set of dominance interactions, thereby avoiding the bias introduced by imputation procedures. Using this approach, we reveal heretofore-unappreciated levels of orderliness in animal groups.

Our approach is based on the triad census, a tool commonly used in social network analysis to count directly the frequencies of all triadic configurations in the data (Figures 1 & A1; Holland and Leinhardt, 1970, 1976; Wasserman and Faust, 1994; Faust, 2007). The triad census allows us simply to compare the frequencies of transitive and cyclic triads. The relative frequencies of triadic configurations, or 'motifs' are routinely used to characterize the structural properties of networks (Kendall and Babington Smith, 1940; Harary and Moser, 1966; Holland and Leinhardt, 1976; Frank and Harary, 1982; Karl-

Table 1. Operational definitions of terms

<i>Cycle*</i>	— A particular form of triad in which directional relations form a cycle, e.g. A dominates B, B dominates C, and C dominates A ($A > B > C > A$). In a <i>tournament</i> , all intransitive triads are cycles.
<i>Imputation</i>	— A general term for procedures to substitute a missing data point with some value.
<i>Linear hierarchy</i>	— Dominance structure fulfilling two criteria: (1) all dyads have a dominant-subordinate relation, and (2) all triadic relations are transitive. Synonyms: <i>complete acyclic digraph</i> , <i>peck order</i> , <i>transitive tournament</i> .
<i>Linearity</i>	— A generic term to describe one of two indices: Kendall's <i>K</i> and Landau's <i>h</i> . These both describe how close the structure of dominance relation is to a linear hierarchy. See Methods for details on the indices.
<i>Orderliness</i>	— The tendency of triadic relationships to be ordered, or transitive. By our definition, <i>linearity</i> and <i>triangle transitivity</i> are both measures of orderliness.
<i>Tournament</i>	— A directed network composed purely of asymmetrical dyads. Synonym: <i>Round robin tournament</i> .
<i>Transitive triad*</i>	— A set of three nodes that are all connected to each other, in which the asymmetrical relationships are transitive (if $A > B$ and $B > C$, then $A > C$). Synonyms: <i>ordered triple</i> .
<i>Transitivity*</i>	— Generically, the proportion of a given set of triads that are transitive. Mathematically, it can be defined in several different ways for directed and undirected networks (e.g., see Holland and Leinhardt, 1976; Frank and Harary, 1982; Karlberg, 1999).
<i>Triangle</i>	— A set of three nodes, each of which is connected to the other two. Synonym: <i>closed triad</i> , <i>complete triad</i> .
<i>Triangle Transitivity</i>	— An index based on the proportion of transitive triangles among all triangles in a network.

* These terms have different definitions when applied to undirected networks.

berg, 1999; Milo et al., 2002; Faust, 2008; Allesina and Levine, 2011). Here, we build on this body of work to define a metric (P_t) that quantifies the proportion of transitive triads among all 'triangles' (those triads in which all dominance relations were established and thus could potentially be transitive). We will first show that the expectation for P_t in a random network is 0.75, regardless of group size or matrix sparseness. Using this expectation as the baseline, we develop a scaled index of 'triangle transitivity' (t_{tri}). Measures of linearity and triangle transitivity take different approaches to describe an essential component of dominance hierarchies: the tendency of triadic relations to be ordered (i.e. transitive) rather than cyclic. Linearity (K and h indices) describes the transitivity of dominance relations in the context of tournaments, whereas triangle transitivity (t_{tri}) is the transitivity of the subset of triads in which all dominance relations were observed. These both differ slightly from other measures of transitivity (Holland and Leinhardt, 1976; Frank and Harary, 1982; Karlberg, 1999). Because the terms 'linearity', 'transitivity' and 'triangle transitivity' all refer to distinct methods for measuring the tendency of triadic relations to be ordered (Table 1), we will use the general term 'orderliness' to refer to this family of metrics. Our goals are to use a network approach to illuminate some complications related to the analysis of orderliness in dominance relations in animal groups and provide some potential avenues for further exploration of social systems.

Methods

Calculating Measures of Linearity

de Vries (1995) gave a thorough account of two methods of measuring linearity: Kendall's K (originally denoted as ζ ; Kendall and Babington Smith, 1940; Appleby, 1983) and Landau's h (Landau 1951a). With the exception of subtle differences when measuring linearity in groups with even versus odd

numbers of individuals, these two values are nearly identical. Because most current empirical studies of dominance structure use a modified version of Landau’s method (denoted h' : de Vries 1995), we will focus on comparisons between h' and our metric t_{tri} . Nevertheless, an overview of the earlier linearity indices is instructive for purposes of distinguishing them from our index of triangle transitivity.

Kendall’s K is defined as the proportion of cyclic triads observed (d), relative to the maximum possible number of cycles (Kendall & Babington Smith 1940). For a group of N individuals, the dominant–subordinate relations are summarized in a $N \times N$ matrix of dominance scores. For convenience, we will use Appleby’s (1983) criteria for scoring in the dominance matrix. Individuals that win more than 50% of encounters in each dyad receive a score of 1 in its row at the column position of the subordinate. If both individuals win an equal number of encounters, each receives a score of 0.5 in its respective row–column positions. Other criteria for assigning dominance scores are possible. The most appropriate criteria depend on the research subjects and the questions addressed. For each individual i , S_i is the row sum (dominance total) of these scores. Subordination totals are given by the column sums. Kendall & Babington Smith (1940) showed that the number of cyclic triads is

$$d = \frac{N(N-1)(2N-1)}{12} - \frac{1}{2} \sum (S_i)^2 \quad (1)$$

The maximum number of cyclic triads possible among N individuals is

$$\begin{cases} d_{\max} = 1/24 (N^3 - N) & \text{for odd values of } N \\ d_{\max} = 1/24 (N^3 - 4N) & \text{for even values of } N \end{cases} \quad (2)$$

Given these,

$$K = 1 - \frac{d}{d_{\max}} \quad (3)$$

Thus, K is an index of the frequency of cyclic triads relative to the maximum possible. $K = 1$ when no cyclic triads exist, and $K = 0$ when the number of cyclic triads is maximal. Note that the dependence of the measure on whether N is odd or even makes this measure problematic for comparing linearity across groups of differing size.

Landau’s (1951a) approach is based on the variance in dominance among individuals. Maximum variance occurs when the hierarchy is completely linear. Using the same notation as above, Landau’s (1951a) hierarchy index is defined as

$$h = \frac{12}{N^3 - N} \sum_{i=1}^N \left[S_i - \frac{N-1}{2} \right]^2 \quad (4)$$

The value of h also ranges from 0 to 1, with $h = 1$ being perfect linearity. Values of K and h are equal for odd-sized groups but differ slightly for even-sized groups.

Both Kendall’s K and Landau’s h are derived from analyses of tournaments. When null dyads occur, K and h are biased towards underestimating linearity (Appleby, 1983; de Vries, 1995). Currently, a randomization procedure is commonly used whereby dominant (1) versus subordinate (0) scores are randomly imputed to the members of each null dyad. An h value is calculated for this ‘filled’ dominance matrix, and the modified Landau’s h (denoted as h') is the average h value of 10 000 randomly filled matrices (de Vries 1995). This is also the first randomization step in the statistical test advocated by de Vries (1995), which is described later (see Statistical Test of Linearity and Triangle Transitivity).

Calculating the Index of Triangle Transitivity, t_{tri}

Our method for measuring triangle transitivity, t_{tri} , is based on direct enumeration of the triad types without resorting to randomly filling in null dyads. The matrix of dyadic dominance relations is directly equivalent to a network adjacency matrix (Wasserman & Faust 1994), with the slight modification that when two individuals win the same number of contests against each other, they both receive scores of 1 instead of 0.5. In the corresponding network diagram, a dominant–subordinate relation (asymmetric dyad) is represented by an edge (arrow) directed from the dominant to the subordinate node (individual). Null dyads lack a connecting edge. Mutual dyads (two-way arrows), in which both individuals win the same number of contests, are very rare in dominance data sets (on average, 2.2% of dyadic relations were mutual in our sample of 101 empirical networks; Supplementary material, Table S1). Moreover, mutual dyads are necessarily transient states, and can occur only when the dyad has interacted an even number of times. From a methodological standpoint, mutual dyads and null dyads are similar: they both represent an unresolved dyadic relation such that one additional interaction would create an asymmetrical dyad. A more comprehensive treatment of the transitive dynamics of dominance relation would need to account for such complications, but this is beyond the scope of the current study. Here, we first discuss the measurement of triangle transitivity in networks that contains no mutual dyads. We do so because it results in a greatly simplified triad census (Holland & Leinhardt 1976) of seven rather than 16 types, without affecting any of our conclusions. This will allow us to present our approach in its simplest form. However, the approach can be extended to include networks with mutual dyads, and we discuss the calculation of the triangle transitivity in networks with mutual dyads in the Appendix.

A directed network with only asymmetric or null dyads has seven distinct (nonisomorphic) types of triads (Figure 1; see Figure A1 for the 16 types possible with mutual edges; Holland and Leinhardt, 1976; Wasserman and Faust, 1994). Each combination of three nodes (e.g. 165 triads in an 11-animal group) is distributed across these seven possible types. The triad census is implemented in network analysis packages in R (e.g. statnet: Handcock et al. 2003; igraph: Csárdi & Nepusz 2006). Of the seven triad types, we focus particularly on the two triangles (i.e. triads connected by three edges): the transitive and cyclic triangles. The proportion of transitive triangles relative to all triangles (P_t) is given by

$$P_t = \frac{N_{\text{transitive}}}{N_{\text{transitive}} + N_{\text{cycle}}} \quad (5)$$

where $N_{\text{transitive}}$ is the number of transitive triangles, and N_{cycle} is the number of cyclic triangles. Codes for calculating P_t using the statnet package (Handcock et al. 2003) in R (R Development Core Team 2009) are presented in the Supplementary material.

In random networks, P_t is expected to equal 0.75. This property can be demonstrated intuitively by considering all possible triangle configurations between three individuals A, B and C (Figure 2; Appleby 1983). Of eight possible configurations, six, or 75%, are transitive. A mathematical derivation, based on the expected frequencies for random networks (Holland & Leinhardt 1976) is given in the Appendix. Furthermore, the result is easily shown by simulation of a large sample of random networks and calculating P_t .

With an expected value of $P_t = 0.75$, we can scale transitivity so that it runs from 0 for the random expectation to 1 (all triangles are transitive, no cycles). Our triangle transitivity metric, t_{tri} , is then given by

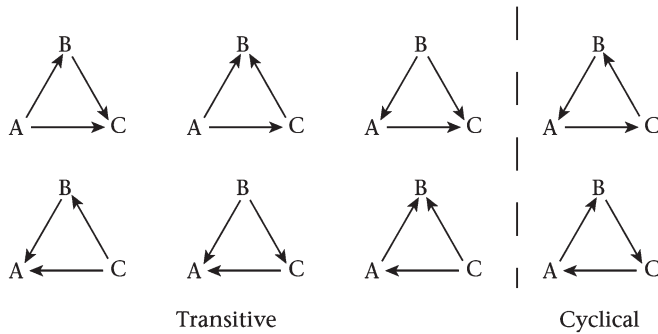


Figure 2. All eight possible patterns of dominant-subordinate relations between individuals A, B and C. Triangles to the left of the dashed line are transitive and those on the right are cyclical. Six of eight, or 75%, of possible triangles are transitive.

$$t_{\text{tri}} = 4(P_t - 0.75) \quad (6)$$

Note that t_{tri} could be negative if more cyclical triangles occurred than would be expected in a random network. Empirical data sets rarely have t_{tri} values that are negative, and even then the values are always close to 0 (Supplementary Table S1).

Triangle transitivity, t_{tri} , can also be calculated for each iteration of the 'random fill' process as described by de Vries (1995; see Calculating Measures of Linearity). We will refer to the average transitivity from these 'filled' networks as t'_{tri} . Comparing h' and t'_{tri} allows us to directly compare the value of linearity and transitivity in imputed networks. Comparing values of t'_{tri} from imputed matrices and t_{tri} from the raw data allows us to disentangle the effect of the imputation procedure itself on measures of dominance structure.

Statistical Analysis of Linearity and Triangle Transitivity

A two-step randomization procedure advocated by de Vries (1995) is the predominant statistical test of significant linearity. In the first step, one imputes a random dominance relation to all null dyads and then calculates an initial linearity, h_0 . In the second step, all dyadic dominant-subordinate relations are randomized. The linearity of this randomized matrix is h_r . These two values, h_0 and h_r , are compared with each other. Steps 1 and 2 are repeated 10 000 times; the one-tailed P value is the proportion of randomizations for which $h_r \geq h_0$. In essence, this procedure compares the linearity of an empirical, although imputed, matrix with the expected linearity from random matrices of the same size. The average value of h_0 from the 10 000 simulations is the h' index (see Calculating Measures of Linearity).

To assess the significance of our transitivity metric we use logic similar to that of de Vries (1995), but the procedure is conducted without imputing null dyads. In network theory, this is called a conditional uniform graph approach (Wasserman and Faust, 1994; Faust, 2010). First, we generate 1000 dyad census-conditioned random graphs; these random networks simulate the dominance structure for hypothesized groups of the same number of individuals and same number of observed dominance relationships, but with uniform probability for each individual dominating any other individual. We then compare the range of triangle transitivity values in these random graphs (t_{random}) to the empirical value, t_{tri} . The one-tailed P value is the proportion of times $t_{\text{random}} \geq t_{\text{tri}}$. The application of this procedure for networks with mutual dyads is discussed in the Appendix. In the Supplementary material, we provide the codes for conducting this procedure using the *statnet* package (Handcock et al. 2003) in R (R Development Core Team 2009).

Comparing Transitivity and Linearity in Random Networks

To assess the effects of network size on measures of linearity and transitivity, we simulated random tournaments (i.e. networks composed entirely of asymmetrical dyads) of varying sizes (range 5–50 nodes), with 1000 replicates for each network size. For replicate random tournaments of a given size, we measured the mean and confidence intervals of h and P_t . Note that in tournaments, there are no null dyads to impute, so $h' = h$. Similarly, in tournaments, $P_t = 1$ represents a completely linear hierarchy because all dyads have a dominant-subordinate relationship, and all dominance relations are transitive. To determine the range of possible P_t values, we also calculated the minimum value of P_t possible in each set of simulations using

$$P_{t\text{min}} = 1 - \frac{d_{\text{max}}}{N_{\text{transitive}} + N_{\text{cycle}}} \quad (7)$$

where d_{max} is the maximum number of cyclic triangles, as defined by equation (2). This calculation only applies to tournaments (Kendall & Babington Smith 1940), as we do not know of any algorithm for calculating the minimum number of transitive triads in sparse networks.

We also investigated the effect of network sparseness (proportion of dyads that are null) on values of P_t by constructing random networks of constant size (20 nodes) but of varying sparseness (range 0–0.9), and plotting the means and confidence intervals of P_t for 1000 replicates of each level of network sparseness. To match the one-tailed statistical test of linearity and triangle transitivity, our confidence interval represents 0 to 95th percentile of h and t_{tri} values in all of our random networks. Values that are outside this range would be considered statistically significant at $\alpha = 0.05$.

Comparing Transitivity and Linearity in Empirical Networks

We collected 101 matrices containing raw win-loss totals from 55 studies published in peer-reviewed journals (Supplementary Table S1). These included studies on invertebrates, fish, birds and mammals, with group size ranging from 6 to 45 individuals. We excluded matrices of five or fewer individuals, and those with fewer than two interactions per individual. Some studies included multiple matrices (either observations of different groups or of the same group at different times), and we included all available matrices that fit our criteria. Although the sample is not exhaustive, it covers a wide range of taxa and hierarchical structures. We first analyse empirical networks in which we exclude mutual dyads because they are rare and pose theoretical complications (see Calculating the Index of Triangle Transitivity above). In the Appendix, we present the method of calculating triangle transitivity in networks with mutual dyads, and show that excluding mutual dyads has negligible effects on the measure of triangle transitivity.

We calculated linearity and triangle transitivity indices from randomly filled dominance matrices (h' and t'_{tri} , respectively), using the procedure described in de Vries (1995; see "Calculating Measures of Linearity" and "Calculating the Index of Triangle Transitivity," above). We implemented the randomization routine in R. We then calculated the scaled index of triangle transitivity (t_{tri}) from empirical matrices using only the raw data presented in the publications (see Supplementary material for codes written in R). Finally, we calculated the P values associated with statistical tests of h' and t_{tri} from the empirical data using the procedure outlined above (see Statistical Test of Linearity and Transitivity).

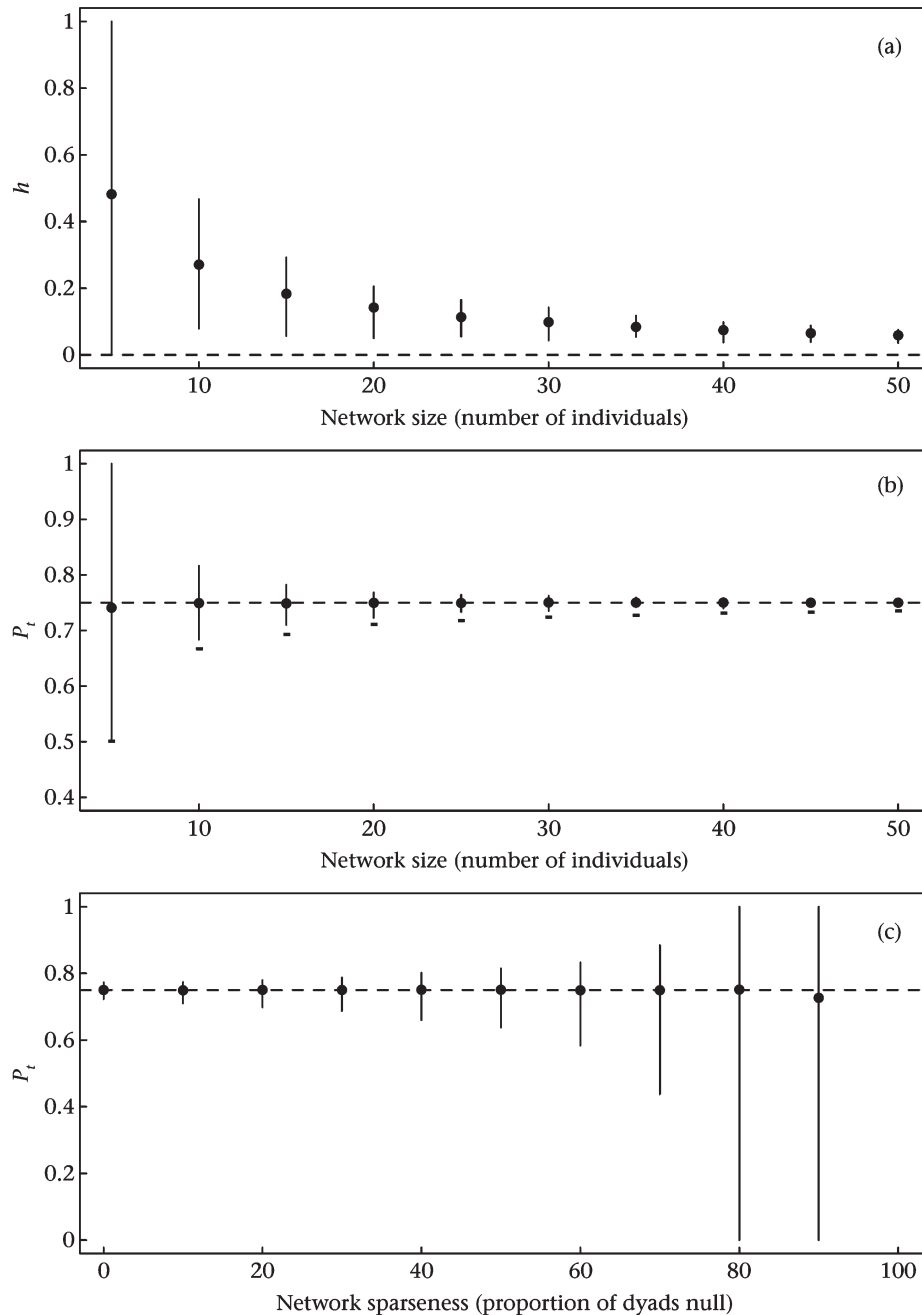


Figure 3. Values of linearity and transitivity in simulated random networks. Symbols represent mean values of (a) h or (b) P_t from 1000 simulated random tournaments of varying sizes, or (c) mean values of P_t from 1000 simulated random networks of $N = 20$ individuals and varying sparseness. We did not calculate h in sparse networks. Lines represent the 0 to 95th percentile of h and P_t values for replicate simulated networks of each size or density. Dotted line represents $h = 0$ in (a), and $P_t = 0.75$ in (b, c). In (b), the horizontal bars represent the minimum level of transitivity possible in a tournament of a given size, calculated by equation (7). Average values of Landau’s h change with network size, but average values of P_t do not change with network size or sparseness. Variance of both h and P_t decrease with increasing network size, and variance of P_t also increases in networks with more null dyads. Minimum levels of transitivity in sparse networks cannot be calculated analytically. Small, sparse networks are not amenable to statistical tests of social structure because the variance in expected values is large, and even perfect linearity or transitivity would not differ significantly from random.

General Statistical Methods

We investigated the effects of network size and network sparseness on measures of linearity and triangle transitivity using linear regression. Network size was log transformed, and network sparseness was arcsine square root transformed to conform to normality assumptions for linear regression. All statistical and simulation procedures were conducted in R.

Results

Triangle Transitivity and Linearity in Random Networks

We first evaluated how network size (number of individuals in the group) affected the random expected values of h and P_t (Figure 3a, b). We confirmed that network size affected the h estimate of linearity in random tournaments: the expected

values of h decreased with increasing group size (Figure 3a; Landau 1951a). In contrast, the average proportion of transitive triads (P_t) remained constant at 0.75 over various network sizes (Figure 3b). The 95% confidence intervals shown in Figure 3 illustrate the range of h and P_t values that could arise by chance (for one-tailed tests at $\alpha = 0.05$). The confidence interval is larger for smaller tournaments, and includes $h = 1$ or $P_t = 1$ in tournaments of five individuals, showing that perfectly linear hierarchies often arise by chance in very small groups. Similarly, the average value of P_t also stayed constant at 0.75 at different levels of network sparseness, but the 95% confidence interval increased when the network was very sparse (Figure 3c).

The change in expected values of h also means that the interpretation of dominance structure at a given value of h could vary depending on group size. For example, $h = 0.4$ at $N = 5$ individuals is not significantly different from the random expectation, but $h = 0.4$ at $N = 40$ would be considered significantly linear.

In summary, while the statistical probability of a given value of h and P_t arising by chance are both affected by network size, only P_t serves as a reliable indicator of the sign (positive or negative) of the orderliness of dominance structure relative to random expectation. In particular, $P_t > 0.75$ always indicates that there are more transitive triangles than the null expectation. We therefore scale our index of triangle transitivity, t_{tri} (equation 6), relative to 0.75. However, the magnitude of the t_{tri} value is not necessarily informative as a statistical index in and of itself because the confidence intervals around this expected value vary with network size and density.

Triangle Transitivity and Linearity in Empirical Networks

To determine whether linearity and triangle transitivity measures yield fundamentally different estimates of social structure, we simultaneously calculated h' and t'_{tri} from 10 000 replicates of each of the 101 empirical data sets whose null dyads we filled randomly. The objective was to compare the indices under the same conditions of random filling. The linearity and transitivity indices were tightly correlated (Pearson's correlation: $r_{99} = 0.98$, $N = 101$ matrices, $P < 0.001$), but the best-fit curve to explain the relationship between the two measures was nonlinear (second-degree polynomial: $y = -0.02 + 0.35 \times x + 0.70 \times x^2$; Supplementary Figure S1). The nonlinear relationship means that the two indices are not interchangeable. The nonlinearity is most likely the result of how the values of the two indices differ in response to changing network size (Figure 3a, b). To support this claim, linear regression with h' , but with network size included as a covariate, explained 99% of the variation in the value of t'_{tri} ($F_{3,97} = 4286$, $R^2_{\text{adj}} = 0.99$, $P < 0.001$), a significantly better fit compared to the model that did not include network size (Wald test: $F_{2,98} = 254.6$, $P < 0.001$; linear model without network size: $F_{1,99} = 2016$, $R^2_{\text{adj}} = 0.95$, $P < 0.001$). That result suggests that under the same constraints (i.e. when all dyads are randomly assigned a dominance relation and when network size is included as a covariate), t'_{tri} and h' are essentially equivalent measures.

We then compared triangle transitivity, $t_{\text{tri}'}$ from empirical networks with unmanipulated null dyads, with $t'_{\text{tri}'}$ where null dyads were randomly filled. Comparing $t_{\text{tri}'}$ and $t'_{\text{tri}'}$ allowed us to investigate the effect of the random-fill imputation procedure used in calculating the h' linearity index.

The triangle transitivity, $t_{\text{tri}'}$ in the unmodified dominance data sets was greater than $t'_{\text{tri}'}$ in the randomly filled data, indicating that the imputation procedure leads to overly conservative estimates of orderliness (mean \pm SE: $t_{\text{tri}'} = 0.88 \pm 0.02$; $t'_{\text{tri}'} = 0.53 \pm 0.03$; Wilcoxon signed-ranks test: $Z = 8.2$, $P < 0.001$;

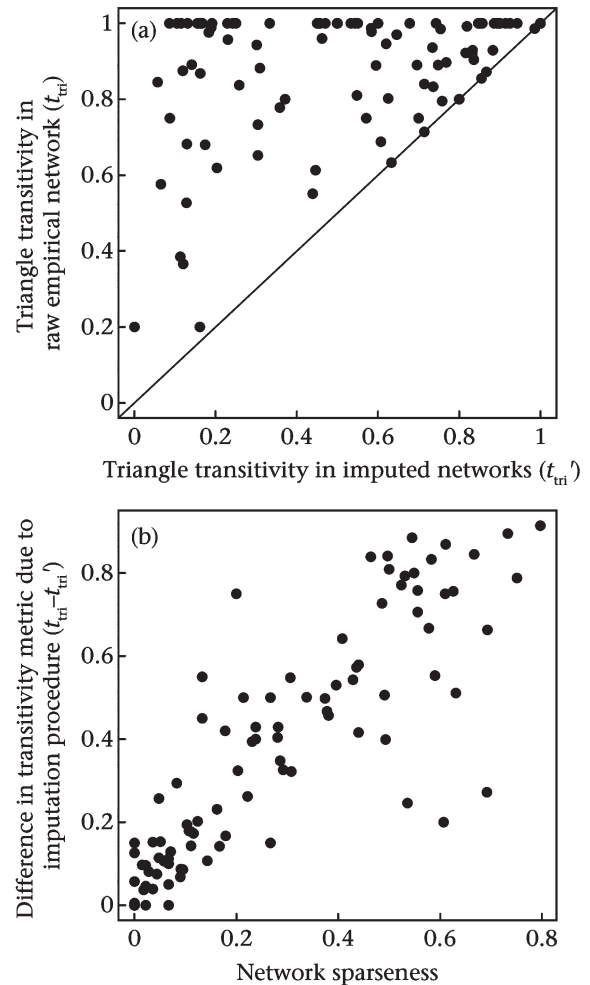


Figure 4. Randomly filling in null dyads reduces the transitivity value of social dominance networks. (a) Comparison of filled versus raw dominance networks shows that triangle transitivity in randomly filled networks (t'_{tri}) is systematically lower than when triangle transitivity is calculated without manipulating the data (t_{tri}). (b) Amount of discrepancy between imputed and raw networks is explained by the proportion of dyads that were imputed. Note that some overlapping data points exist.

Figure 4a). The reduction in triangle transitivity associated with imputation is related to the proportion of null dyads (linear regression: $F_{1,99} = 304.1$, $R^2_{\text{adj}} = 0.75$, $P < 0.001$; Figure 4b). Of the 101 data sets, 88 (87%) contained at least one null dyad, and the proportion of null dyads (mean \pm SE = 0.26 ± 0.02) was positively correlated with the number of individuals (Pearson's correlation: $r_{99} = 0.46$, $N = 101$, $P < 0.001$). Moreover, 33 (33%) of the 101 data sets contained no cyclic triads ($P_t = t_{\text{tri}} = 1$), while only four of the 101 had an h value of 1. Thus, filling in null dyads artificially creates cyclic triads and systematically underestimates orderliness. Because null dyads tend to be more abundant in studies of larger groups, the apparent decrease in linearity with increasing group size is most likely an artefact of the imputation procedure used in calculating h' .

We used linear regression to confirm that group size and proportion of null dyads alone explain most of the variation in the linearity metric, h' (full model with network size and sparseness as covariates: $F_{3,100} = 149.2$, $R^2_{\text{adj}} = 0.82$, $P < 0.001$). Specifically, estimated linearity decreases with increasing network size or sparseness (Supplementary Figure S2a, b). In contrast, our transitivity metric, $t_{\text{tri}'}$ was unaffected by either

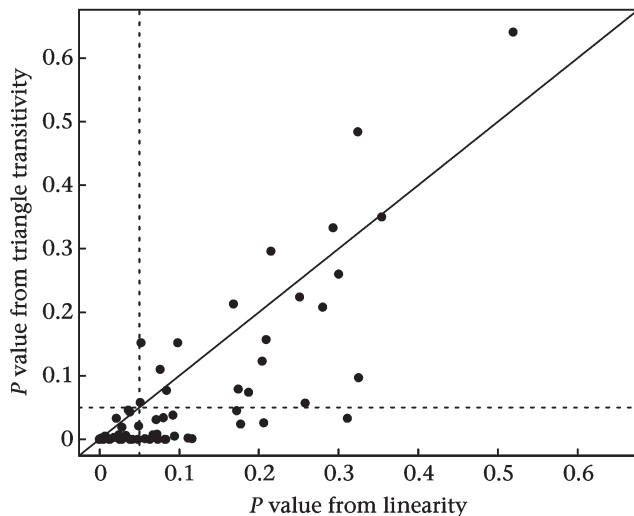


Figure 5. Comparison of P values from linearity and transitivity measures. Statistical analysis of linearity followed de Vries (1995). Solid line is a 1:1 line, and dotted lines indicate $\alpha = 0.05$ for each axis. Imputed linearity often underestimates the statistical significance of social orderliness. Of 101 empirical dominance networks analysed, 15 that would have been interpreted as nonlinear actually had significant levels of transitivity at $\alpha = 0.05$ (one-tailed simulation test for both). Note that some overlapping data points exist.

network size or sparseness (Supplementary Figure S2c, d; linear regression, full model with size and sparseness as covariates: $F_{3,100} = 0.32$, $R^2_{\text{adj}} = -0.02$, $P = 0.81$). Therefore, it is probably a more unbiased measure of social orderliness that is amenable to comparisons across studies.

The imputed metric of linearity, h' , could lead to various misinterpretations of social orderliness in animal groups. While the P values derived from the linearity and transitivity procedures were correlated (Pearson's correlation: $r_{99} = 0.85$, $N = 101$, $P < 0.001$), the P values for linearity were larger (i.e. less significant) than those for triangle transitivity (Wilcoxon signed-ranks test: $Z = -7.4$, $P < 0.01$; Figure 5), suggesting that imputation-based linearity underestimates the threshold for significant social orderliness. Thus, 15 of the 101 data sets in which the linearity failed to detect significant structure were deemed significantly nonrandom using triangle transitivity ($\alpha = 0.05$), whereas only one data set was significantly linear but marginally nonsignificant with triangle transitivity (Figure 5). Some studies, especially those with large, sparse matrices, might therefore conclude that groups contain no significant hierarchical structure if relying on the linearity index, h' , even when the triadic relationships that actually exist are disproportionately transitive.

Discussion

In this study, we define triangle transitivity (t_{tri}) as a scaled index of the relative frequency of transitive triads among all triangles (closed triads) in a dominance network. This allows us to ask the question: of the three-way dominance relationships we actually observed, what proportion of these are transitive rather than cyclic? Our method is based on the triad census, a network analysis tool that allows us to count the frequencies of all triadic configurations in the network. We show that in tournaments of the same size, t_{tri} and the linearity index h both describe the degree to which triadic relations are transitive. Discrepancies between measures of linearity and triangle transitivity can arise when null dyads occur, with the linearity metric, h' , becoming

increasingly conservative with the proportion of null dyads. This is because the imputation procedure used to calculate linearity of incomplete networks (h') creates triangles that do not exist in the observed data set, thus obscuring the actual triangle relationships that occurred. This effect is magnified with increasing group size because large matrices are more likely to be sparse. Sparse networks are ubiquitous: in our sample, 87% of dominance networks had at least one null dyad, and on average 26% of dyads were null. Of the 43 of 101 data sets in which t_{tri} equalled 1, only four were complete tournaments that could be considered unequivocally linear. We determined that 15 dominance hierarchies that had significantly high levels of triangle transitivity would not be considered significantly linear using the h' criterion (Figure 5). We argue that dominance relations in these groups are nonrandomly transitive. The decrease in h' associated with increasing group size is therefore largely explained by two factors: the average value of h in randomized networks decreases with increasing group size, and large groups tend to contain more null dyads. In effect, social dynamics at the level of triads seems relatively unaffected by overall group size, such that triangle transitivity often remains high even in large groups. Thus, our findings emphasize even more strongly than heretofore appreciated the striking orderliness of most animal societies.

In the current study, we have scaled the triangle transitivity index relative to the null expected value. This scaling procedure presents some advantages and drawbacks. The major advantage of the t_{tri} index is that it is scaled relative to a value that is constant regardless of network size or sparseness. The expected value of t_{tri} is always 0, and the maximum value is 1, in all directed networks. Negative values of the t_{tri} index are possible, but the exact minimum value, which will vary with network size and sparseness, is unknown. In the current study, we simply scaled t_{tri} so as to be positive when triangles were more frequently transitive than average, and we scaled t_{tri} to be negative when triangles were more frequently cyclic than the random expectation. The effect of network size and density on the bounds of indices of network structure is a general problem in network theory (Butts, 2006; Faust, 2010), and further work is needed to define precisely the bounds of triangle transitivity in sparse networks.

Our approach complements, but does not replace, other approaches to understanding the structure of dominance hierarchies. For example, we followed convention and assigned dominant-subordinate relations based on which individual won more than 50% of encounters, but this is most likely an oversimplification. Methods such as the directional consistency index (van Hooff & Wensing 1987), a measure of how consistently one individual wins against another individual, may be useful for investigating the stability of dyadic relations. Moreover, there are other important dynamics of dominance relations that are not captured by the triangle transitivity metric. For example, even when all triangles are transitive ($P_t = t_{\text{tri}} = 1$), longer-range cycles (e.g. $A > B > C > D > A$) could occur, and these individuals cannot be arranged in orderly dominance ranks. Nevertheless, we focus on triads because it is the smallest unit of transitivity, and because the analysis of triads has been well established (Holland and Leinhardt, 1976; Faust, 2007) and it offers ready comparison with existing measures of linearity. Other, more comprehensive network methods to analyse dominance data may be appropriate for some questions (Iverson & Sade 1990). One such example is the dominance-directed tree method for generating graphical representations of nonlinear hierarchies (Izar et al. 2006). Similarly, more sophisticated measures of social structure that incorporate temporal and spatial dynamics are possible (Whitehead, 1997; Hemelrijk, 2000). Such dynamics are also central to network theory as well as studies of animal dominance.

A major question remains: why do some pairs establish clear dominance relations while other pairs fail to interact? If patterns of noninteractions are not random, then this could bias the formation of transitive versus cyclic triangles. For example, if two individuals can infer their relative dominance status without interactions (e.g. via long-distance social signals), then individuals may avoid interacting with others when they are more likely to become entangled in an irresolvable cyclic triad. Third-party effects such as eavesdropping (Earley and Dugatkin, 2002; Mennill and Ratcliffe, 2004) can also affect whether certain individuals interact aggressively or avoid each other. Alternatively, some dyadic interactions may not be worth the cost of aggression, for example, if two similarly low-ranked individuals gain little benefit from outranking each other. With third-party effects and high-stakes contests, some individuals may avoid forming transitive triangles because the probable outcome of the contest is inferred through previous observations. Spatial segregation or other mechanisms that make it impossible for two individuals to interact (called structural zeros in de Vries 1995) would also affect which triads are closed, but whether this would bias triangle transitivity is not immediately clear. Theoretical models of the ecological and evolutionary processes that lead to particular patterns of 'triad closure' (Rapoport, 1953; Kossinets and Watts, 2006) will be important avenues of research to understand how highly transitive social dominance networks arise. Regardless of what mechanisms mediate competitive interactions, we suggest that patterns of noninteractions are critical to understanding social organization.

Social dominance is a dynamic process, and a network approach provides an opportunity to explore how social structure changes across time (Kossinets & Watts 2006). Early sequences of dominance interactions can have profound effects on later interactions, as well as the global structure of the dominance network (e.g. winner and loser effects: Landau, 1951b; Dugatkin, 1997). For example, Chase (1982b) showed that in chickens, the potential levels of transitivity were largely determined by the early sequences of triadic interactions (i.e. when two out of the three dyads in a triad had established dominance relations). That is, two-edge configurations that ensured transitivity (i.e. 'Double-dominant' and 'Double-subordinate' in Figure 1) were more common than the only two-edge configuration that could potentially lead to cycles (i.e. 'Pass-along' in Figure 1). This imbalance between transitive and cyclic precursors at the two-edge stage formed the basis of the sequential development model of hierarchy formation (Chase, 1982b, 1985; Chase and Rohwer, 1987). The triad census provides a way to explore these dynamics efficiently on the level of the entire network through time. Because social interactions can often be observed in real time, sequential analyses of network structure should be a promising approach to connect these important lower-level processes (Faust 2007) to the patterns of hierarchical organization in dominance relations.

In general, the study of dominance hierarchies fits into a broad context of structure and transitivity in networks, a topic that unites physics, sociology, biology and other disciplines (Rapoport, 1953; Watts and Strogatz, 1998; Milo et al., 2002; Barabási, 2009). Network analyses play an important and increasing role in exploring the structure of animal societies (Krause et al., 2007; Wey et al., 2007; Sih et al., 2009). We anticipate that observations of nonhuman animal social systems in natural and experimental contexts will have much to contribute to the general understanding of the processes that lead to orderly social structures in nature.

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Appendix 1.

Deriving the Expected Value of P_t in Random Networks

In this study, we use a simulation approach to generate the distribution of P_t under the assumption of random dominance relations. The distributions of expected frequencies of triadic configurations for random graphs conditioned on the number of mutual, asymmetrical and null dyads (termed U|MAN distribution) was derived by Holland & Leinhardt (1976). We can use this to simply derive the average expected value of P_t : the proportion of triangles that are transitive. Following Holland & Leinhardt (1976),

$$E_{(030C)} = \frac{1}{4} \frac{A^{(3)}}{k^{(3)}} \quad (\text{A1})$$

$$E_{(030T)} = \frac{3}{4} \frac{A^{(3)}}{k^{(3)}} \quad (\text{A2})$$

where $E_{(030T)}$ and $E_{(030C)}$ are expected frequencies of transitive and cyclic triangles, A is the number of asymmetrical edges in the network, and k is the number of dyads in network g . The notation $z^{(3)}$ stands for $z \times (z - 1) \times (z - 2)$. The expected value of P_t in random networks, $E(P_t)$ is then:

$$E(P_t) = \frac{E_{(030T)}}{E_{(030T)} + E_{(030C)}} = \frac{3}{4} \quad (\text{A3})$$

Therefore, the expected average proportion of transitive triangles in a directed network is 0.75. This is confirmed independently in the main text using simulations and by a heuristic argument for the six transitive triads among the eight possible ways of adding three edges to a given triad (see Results and Figure 2).

Appendix 2.

Calculating P_t in Networks with Mutual Dyads

In the analysis presented in the main text, we excluded mutual dyads (dyads in which both individuals win the same number of contests) because these dyads are rare and have only slight effects on measurements of triad transitivity. However, our approach is easily extended to include dominance networks with mutual dyads.

We first consider the seven different triangle configurations that are possible in networks with mutual, asymmetrical and null dyads (indicated in black in Figure A1). Following Holland & Leinhardt (1976), each triad configuration is labelled with a three-number code representing the number of mutual, asymmetric and null dyads (Figure A1). When applicable, a fourth character is used to denote distinct configurations that share the same frequencies of dyad types (‘D’ = down, ‘U’ = up, ‘C’ = cycle, ‘T’ = transitive). For example, a transitive triad has no mutual dyads, three asymmetrical dyads and no null dyads, so it is labelled as ‘030T’. This is distinguished from a cyclic triad that also contains only three asymmetrical dyads, labelled ‘030C’. This labelling scheme is referred to as MAN labelling (for mutual, asymmetric and null dyads: Wasserman & Faust 1994).

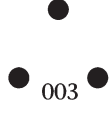

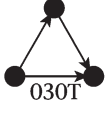
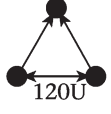
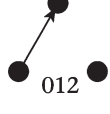
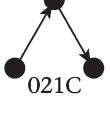
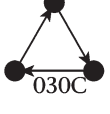
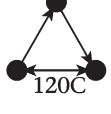
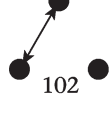
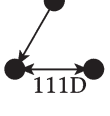
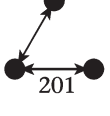
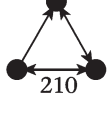

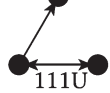
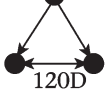
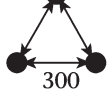
Triad type (T_u)	Transitivity weight (w_u)	Triad type (T_u)	Transitivity weight (w_u)	Triad type (T_u)	Transitivity weight (w_u)	Triad type (T_u)	Transitivity weight (w_u)
	0		0		1		1
	0		0		0		0.5
	0		0		0		0.75
	0		0		1		0.75

Figure A1. Full triad census, showing all 16 triad configurations possible in a directed network. Each configuration is named using the MAN labelling scheme (see text; Holland & Leinhardt 1976). Seven triangle configurations, in which all three nodes are connected by either asymmetric or mutual edges, are shown in black. Weighting factor (w_u) for each of the seven triangle configuration types is based on the probability that the triangle is transitive, with the assumption that each individual in a mutual dyad has equal probability of being dominant. Using these weighting factors, we can calculate the proportion of transitive triangles (P_t) in any directed network (equation A1).

Triads that contain mutual dyads are weighted according to the probability that the configuration is transitive if the mutual dyad becomes a dominant-subordinate relation (Holland and Leinhardt, 1976; Wasserman and Faust, 1994). This is akin to the treatment of mutual dyads in measuring linearity (Appleby, 1983; de Vries, 1995): both individuals are considered to have equal chance of being dominant. For example, triad 120C is weighted by a value of 0.5; the triad may be transitive or intransitive, depending on which member of the mutual dyad dominates, with both scenarios equally probable. Furthermore, 120D and 120U are transitive no matter which individual in the mutual dyad is dominant, so this is weighted by a value of 1. Triad types 210 and 300 are weighted by 0.75 using the same logic. The weighting factors (w_u) of all triad types are presented in Figure A1. Note that P_t cannot be measured if no triangle triads occur.

Applying these transitivity weights to each triad configuration we can now calculate P_t for networks with mutual dyads.

$$P_t = \frac{\sum_u w_u T_u}{N_{\text{triangles}}} \quad (\text{A4})$$

where T_u is the frequency of triad type u , and w_u is the weighting factor for transitivity for triad u . $N_{\text{triangles}}$ is the total number of triangles in the network. The t_{tri} index can be calculated by taking this P_t value and applying equation (6). The P_t values calculated for empirical networks including or excluding mutual dyads were highly correlated ($r_{99} = 0.92$, $N = 101$, $P < 0.001$), and the mean difference in value was 0.006. Therefore, excluding the mutual dyads, at least in this sample of 101 data sets, did not change our results. However, in other networks where mutual dyads are more common, this equation (A1) may be a more appropriate method of calculating P_t .

The statistical procedure for generating a P value for the triangle transitivity of an empirical network is the same as outlined in the main text. For each empirical network, we generate 1000 dyad census-conditioned random graphs and calculate t_{tri} for each. The one-tailed P value is the number of times the t_{tri} value of the random network is greater than the t_{tri} value of the empirical network. In the Supplementary Material, we provide the codes for conducting this procedure in R.

Supplementary Material

Calculation and Statistical Test of Triangle Transitivity

Here, we provide the codes to calculate P_t and t_{tri} and to conduct a statistical test of triangle transitivity of an empirical network using the package 'statnet' (Handcock et al. 2003) in the R programming environment (R Development Core Team 2009). The following codes calculate P_t and t_{tri} in networks using the methods described in Appendix 2.

```
library(statnet)
dat=read.csv("filename.csv",header=TRUE,row.names=1,check.names=FALSE) # read .csv file containing the dominance matrix in binary format
# (dominants = 1, subordinates = 0), with winners as rows and losers as columns.
m=as.matrix(dat)
g=network(m,directed=TRUE)

# We calculate P.t and t.tri for this empirical network.

tri=triad.census(g) #The full triad census as an 16-element vector
w=as.vector(c(0,0,0,0,0,0,0,0,0,1,0,0,1,1,0.5,0.75,0.75)) # The weighting
vector for transitivity
N.triangle=sum(tri*as.vector(c(0,0,0,0,0,0,0,0,0,1,1,0,1,1,1,1,1))) #Count
and sum the number of triangles

Pt=sum(tri*w)/N.triangle
t.tri=4*(Pt-0.75)
Pt
t.tri

## We now conduct 1,000 simulations of random networks with the same
number of mutual, asymmetric and null dyads as the empirical
dominance matrix. We calculate Pt from each of these simulated
networks (r.P.t).

dyads=dyad.census(g)
r=rguman(1000,nv=nrow(m),mut=dyads[1],asym=dyads[2],null=dyads[3])
r.triad=triad.census(r)
r.P.t=apply(r.triad,1,function(x) x[9]/(x[10]+x[9]))

# Finally, we conduct a one-tailed test of the null hypothesis that
P.t of the empirical network is not significantly different from P.t
of the simulated random networks (r.P.t). The P-value is the number
of times r.P.t is greater or equal to the empirical P.t value. By
convention, we reject the null hypothesis if P < 0.05

p=length(r.P.t[r.P.t>=Pt])/1000
p
```

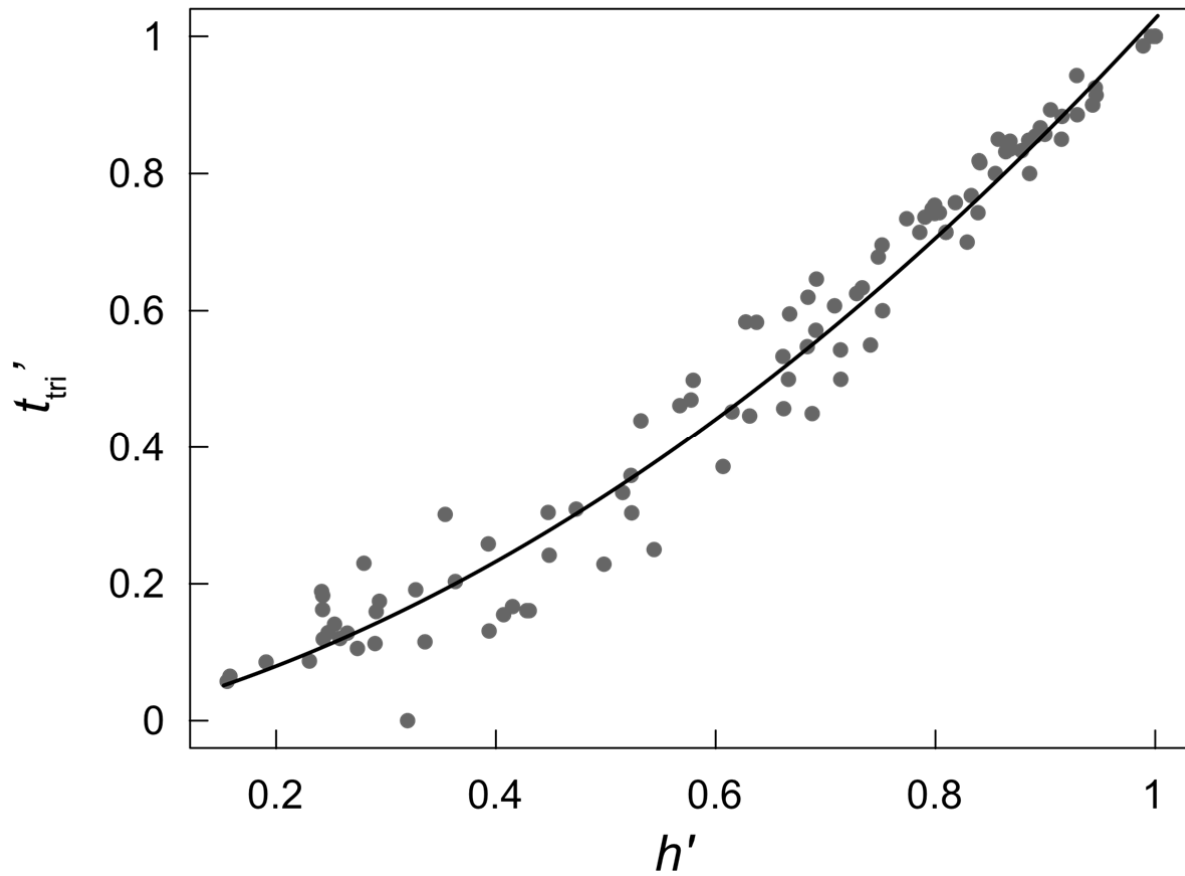


Figure S1. Relationship between t'_{tri} and h' measured using simulations to fill in null dyads from empirical matrices. The line is a polynomial regression line ($Y = -0.02 + 0.35 \times X + 0.70 \times X^2$; $F_{2,98} = 1491$, $R^2_{adj} = 0.97$, $P < 0.001$). The two values are closely related but not directly proportional because the exact relationship between the two indices depends on the size of the network (i.e. the number of individuals).

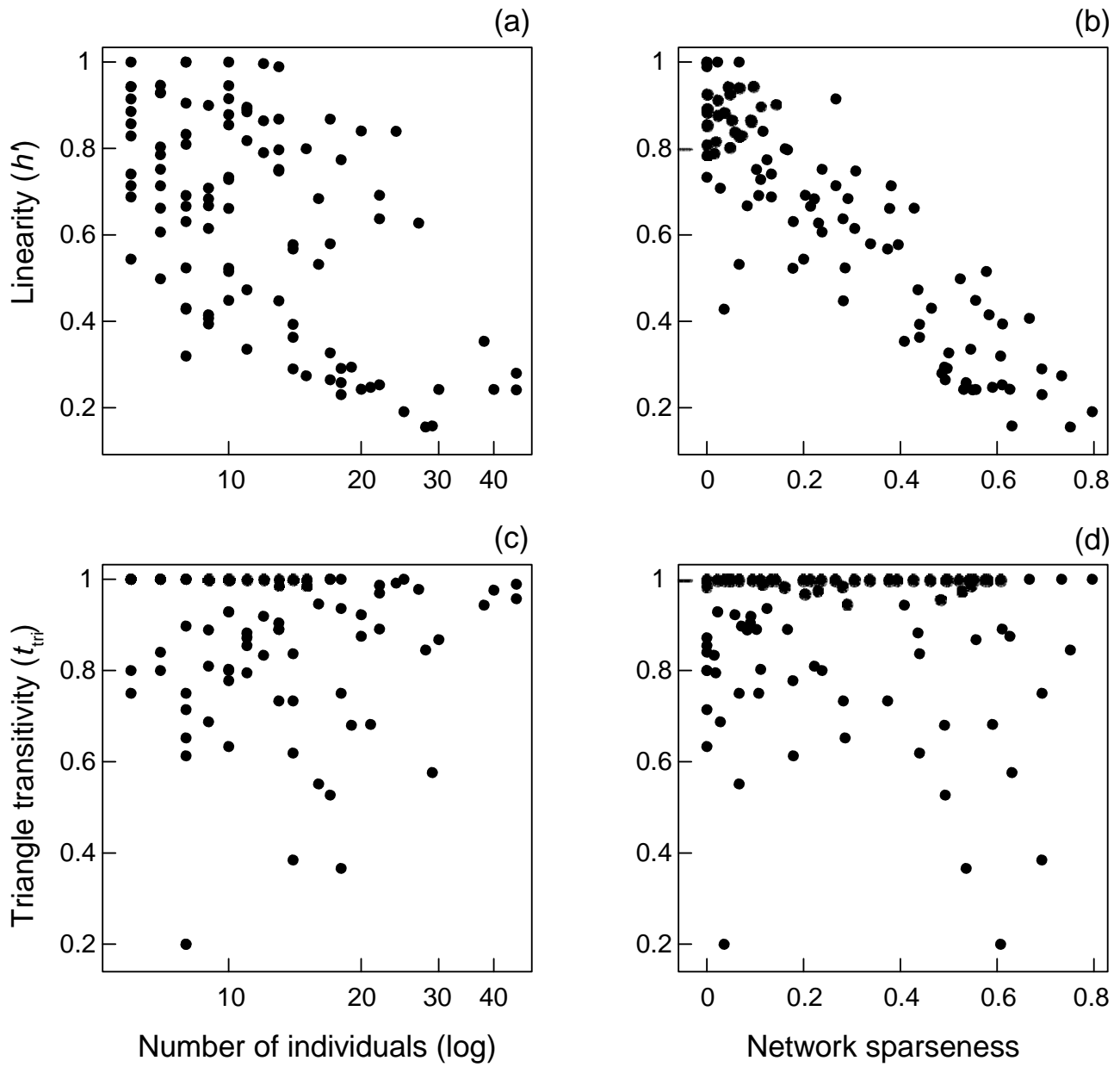


Figure S2. Measures of linearity and triangle transitivity in relation to network size (number of individuals) and network sparseness (proportion of dyads with unknown dominance relationship). (a, b) The linearity measure, h' , decreases with increasing numbers of individuals and proportions of dyads unknown. This bias is created by the process of filling in null dyads with random dominance relationships. (c, d) Triangle transitivity, t_{tri} , is not affected by the number of individuals or the proportion of dyads known.

Table S1Empirical dominance matrices used for analysis of t_{tri} , t_{tri}' and h'

Source	Network		P_t	t_{tri}	t_{tri}'	h'	P value	
	Size	Sparseness					h'	t_{tri}
Allee & Dickinson 1954, Table 3	10	0.378	1.000	1.000	0.533	0.661	0.012	0.000
Appleby 1983, Figure 1	7	0.381	1.000	1.000	0.543	0.714	0.098	0.152
Archie et al. 2006, Figure 2 (GB)	11	0.545	1.000	1.000	0.115	0.335	0.311	0.033
Archie et al. 2006, Figure 2 (A)	8	0.214	1.000	1.000	0.500	0.666	0.094	0.005
Archie et al. 2006, Figure 2 (AA)	10	0.556	1.000	1.000	0.242	0.449	0.174	0.079
Archie et al. 2006, Figure 2 (CB)	6	0.067	1.000	1.000	1.000	1.000	0.021	0.033
Archie et al. 2006, Figure 2 (FB)	6	0.133	1.000	1.000	0.450	0.688	0.258	0.057
Archie et al. 2006, Figure 2 (JA)	7	0.429	1.000	1.000	0.457	0.662	0.168	0.213
Archie et al. 2006, Figure 2 (OA)	9	0.611	1.000	1.000	0.131	0.394	0.354	0.350
Archie et al. 2006, Figure 2 (PC)	9	0.667	1.000	1.000	0.155	0.407	0.324	0.484
Archie et al. 2006, Figure 2 (SI)	6	0.067	1.000	1.000	0.900	0.943	0.036	0.046
Barrette & Vandal 1986, Table 2	20	0.058	0.981	0.922	0.816	0.840	0.000	0.000
Berman et al. 2004, Appendix A	22	0.203	0.992	0.970	0.646	0.692	0.000	0.000
Berman et al. 2004, Appendix B	22	0.281	0.997	0.987	0.583	0.637	0.000	0.000
Berman et al. 2004, Appendix C	18	0.124	0.984	0.936	0.734	0.774	0.000	0.000
Bonanni et al. 2007, Table 1	13	0.282	0.933	0.733	0.304	0.448	0.025	0.000
Bonanni et al. 2007, Table 2	14	0.374	0.990	0.960	0.462	0.567	0.000	0.000
Cafazzo et al. 2010, Table 5	27	0.231	0.994	0.978	0.584	0.627	0.000	0.000
Cheney 1977, Table 1a	12	0.000	1.000	1.000	1.000	0.997	0.000	0.000
Cheney 1977, Table 1b	12	0.015	0.958	0.833	0.736	0.790	0.000	0.000
Clutton-Brock et al. 1976, Table 3	17	0.051	1.000	1.000	0.847	0.868	0.000	0.000
Collias & Taber 1951, Table 3	9	0.583	1.000	1.000	0.167	0.415	0.300	0.260
Collias Taber 1951, Table 4	8	0.464	1.000	1.000	0.161	0.430	0.325	0.097
Collias Taber 1951, Table 5	14	0.440	0.905	0.619	0.203	0.363	0.071	0.002

Source	Network		P_t	t_{tri}	t_{tri}'	h'	P value	
	Size	Sparseness					h'	t_{tri}
Côté 2000, Table A1	38	0.408	0.986	0.943	0.301	0.354	0.000	0.000
Côté 2000, Table A2	40	0.531	0.994	0.976	0.183	0.242	0.000	0.000
Côté 2000, Table A3	45	0.549	0.997	0.989	0.189	0.241	0.000	0.000
Côté 2000, Table A4	45	0.486	0.989	0.957	0.230	0.280	0.000	0.000
Farentinos 1972, Table 1A	6	0.267	1.000	1.000	0.500	0.714	0.209	0.157
Farentinos 1972, Table 1B	8	0.286	0.913	0.652	0.304	0.524	0.172	0.045
Farentinos 1972, Table 1C	8	0.607	0.800	0.200	0.000	0.320	0.519	0.641
Farentinos 1972, Table 1D	11	0.436	0.971	0.882	0.309	0.473	0.067	0.007
Farentinos 1972, Table 1E	6	0.000	0.950	0.800	0.800	0.886	0.051	0.058
Fournier & Festa-Bianchet 1995, Figure 3	30	0.556	0.967	0.868	0.162	0.242	0.000	0.000
Fournier 1995 & Festa-Bianchet, Figure 2	21	0.590	0.920	0.682	0.129	0.247	0.048	0.000
Frank 1986, Table 1	25	0.797	1.000	1.000	0.086	0.191	0.072	0.008
Hartzler 1970, Table 1	7	0.095	1.000	1.000	0.914	0.946	0.007	0.005
Hass & Jenni 1991, Table 1	15	0.733	1.000	1.000	0.105	0.274	0.204	0.123
Hass & Jenni 1991, Table 2	18	0.497	1.000	1.000	0.159	0.291	0.063	0.000
Hass & Jenni 1991, Table 3	17	0.500	1.000	1.000	0.191	0.327	0.041	0.000
Heitor & Vicente 2010, Table 2	6	0.000	1.000	1.000	0.850	0.857	0.049	0.021
Heitor et al. 2006, Table 3	11	0.000	0.964	0.855	0.855	0.891	0.000	0.000
Hewitt et al. 2009, Figure A1 (SH1995)	14	0.440	0.959	0.837	0.258	0.393	0.038	0.000
Hewitt et al. 2009, Figure A1 (P2004)	7	0.000	1.000	1.000	0.943	0.929	0.005	0.000
Hewitt et al. 2009, Figure A1 (PO2004)	7	0.238	0.950	0.800	0.371	0.607	0.206	0.026
Hewitt et al. 2009, Figure A1 (P2005)	9	0.222	0.952	0.810	0.548	0.683	0.018	0.003
Hirotsu 1994, Table 1	13	0.090	0.976	0.904	0.836	0.868	0.000	0.000
Isbell & Pruet 1998, Figure 1A	9	0.306	1.000	1.000	0.452	0.615	0.057	0.001
Isbell & Pruet 1998, Figure 1B	17	0.493	0.882	0.527	0.128	0.265	0.111	0.002
Izar et al. 2006, Table 2	17	0.338	1.000	1.000	0.499	0.580	0.000	0.000
Koenig et al. 2004, Table 1b	7	0.048	1.000	1.000	0.743	0.804	0.024	0.007

Source	Network		P_t	t_{tri}	t_{tri}'	h'	P value	
	Size	Sparseness					h'	t_{tri}
Lahti et al. 1994, Table 1A	6	0.067	0.938	0.750	0.700	0.829	0.084	0.077
Lahti et al. 1994, Table 1C	8	0.071	0.974	0.897	0.768	0.833	0.002	0.002
Lu et al. 2008, Figure 1c(1)	13	0.103	0.973	0.890	0.696	0.751	0.000	0.000
Lu et al. 2008, Figure 1c(2)	13	0.167	0.973	0.890	0.748	0.797	0.000	0.000
McMahan & Morris 1984, Table 1	10	0.178	0.944	0.778	0.358	0.523	0.073	0.000
Marler 1957, Table 1b	8	0.000	1.000	1.000	1.000	1.000	0.000	0.000
Masure & Allee 1934, Table 1	13	0.000	0.997	0.986	0.986	0.989	0.000	0.000
Masure & Allee 1934, Table 2	11	0.018	0.949	0.795	0.758	0.818	0.000	0.000
Masure & Allee 1934, Table 3	7	0.000	0.960	0.840	0.714	0.786	0.033	0.006
Møller 1987, Table 1	13	0.308	1.000	1.000	0.678	0.748	0.000	0.000
Møller 1987, Table 2	10	0.044	1.000	1.000	0.925	0.946	0.000	0.000
Møller 1987, Table 3	14	0.396	1.000	1.000	0.470	0.578	0.001	0.000
Monnin & Peeters 1999, Table 1	6	0.200	1.000	1.000	0.250	0.544	0.280	0.208
Murray 2007, Table 5	18	0.693	0.938	0.750	0.087	0.230	0.177	0.024
Nakano 1994, Table 1	11	0.036	1.000	1.000	0.848	0.885	0.000	0.000
Natoli & De Vito 1991, Table 2	14	0.692	0.846	0.385	0.113	0.290	0.215	0.296
Owens & Owens 1996, Figure 1	7	0.238	1.000	1.000	0.600	0.752	0.080	0.034
Paoli et al. 2006, Table 2	8	0.036	0.800	0.200	0.161	0.428	0.251	0.224
Paoli et al. 2006, Table 3	6	0.267	1.000	1.000	0.850	0.915	0.052	0.152
Parsons & Baptista 1980, Table 4	8	0.000	0.929	0.714	0.714	0.810	0.006	0.004
Patterson 1977, Figure 5	18	0.536	0.842	0.366	0.120	0.258	0.092	0.038
Patterson 1977, Figure 6	28	0.751	0.961	0.845	0.057	0.155	0.116	0.001
Poisbleau et al. 2006, Figure 2a	16	0.067	0.888	0.551	0.439	0.532	0.000	0.000
Poisbleau et al. 2006, Figure 2b	19	0.491	0.920	0.680	0.174	0.294	0.028	0.000
Richter et al. 2009, Table 1	9	0.028	0.922	0.688	0.607	0.708	0.005	0.001
Robbins 2008, Table 2	8	0.179	0.903	0.613	0.446	0.631	0.071	0.031
Rutberg 1986, Table 1	22	0.610	0.973	0.891	0.141	0.253	0.026	0.000

Source	Network		P_t	t_{tri}	t_{tri}'	h'	P value	
	Size	Sparseness					h'	t_{tri}
Rutberg 1986, Table 2	29	0.631	0.894	0.576	0.065	0.158	0.083	0.000
Satoh & Ohkawara 2008, Table 2c	8	0.143	1.000	1.000	0.893	0.905	0.001	0.000
Satoh & Ohkawara 2008, Table 2d	9	0.083	0.972	0.889	0.595	0.667	0.013	0.000
Satoh & Ohkawara 2008, Table 2e	10	0.578	1.000	1.000	0.333	0.515	0.076	0.110
Setchell & Wickings 2005, Table 4	8	0.000	1.000	1.000	1.000	1.000	0.000	0.000
Setchell & Wickings 2005, Table 3	11	0.000	0.968	0.872	0.867	0.895	0.000	0.000
Smith 1976, Table 1	7	0.048	1.000	1.000	0.886	0.929	0.008	0.004
Somers & Nel 1998, Table 2a	6	0.133	1.000	1.000	0.550	0.741	0.187	0.074
Somers & Nel 1998, Table 2b	8	0.107	0.938	0.750	0.571	0.691	0.028	0.019
Somers & Nel 1998, Table 2c	9	0.111	1.000	1.000	0.857	0.900	0.000	0.000
Tamm 1977, Table 1b	10	0.111	0.951	0.802	0.625	0.728	0.003	0.000
Tarvin & Woolfenden 1997, Table 5	16	0.292	0.986	0.946	0.620	0.684	0.000	0.000
Vervaecke et al. 2000, Table 2	6	0.067	1.000	1.000	0.900	0.943	0.038	0.043
deWaal & Luttrell 1985, Table 1	24	0.116	0.998	0.992	0.819	0.840	0.000	0.000
Watt 1986, Figure 1a	10	0.022	0.982	0.929	0.883	0.915	0.000	0.000
Watt 1986, Figure 1b	10	0.022	1.000	1.000	1.000	1.000	0.000	0.000
Watt 1986, Figure 1c	10	0.000	0.950	0.800	0.800	0.855	0.000	0.000
Watt 1986, Figure 1d	10	0.000	0.908	0.633	0.633	0.733	0.001	0.000
Watt 1986, Figure 1e	10	0.022	0.982	0.929	0.833	0.878	0.000	0.000
West-Eberhard 1986, Table 5	7	0.524	1.000	1.000	0.229	0.498	0.293	0.333
Wittemyer & Getz 2007, Table 1	20	0.626	0.969	0.875	0.119	0.243	0.082	0.000
Wittig & Boesch 2003, Figure 1	15	0.162	0.996	0.985	0.754	0.799	0.000	0.000
Zine & Krausman 2000, Table 1	12	0.091	0.980	0.919	0.832	0.864	0.000	0.000

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