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The network motif architecture of dominance hierarchies

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The widespread existence of dominance hierarchies has been a central puzzle in social evolution, yet we lack a framework for synthesizing the vast empirical data on hierarchy structure in animal groups. We applied network motif analysis to compare the structures of dominance networks from data published over the past 80 years. Overall patterns of dominance relations, including some aspects of non-interactions, were strikingly similar across disparate group types. For example, nearly all groups exhibited high frequencies of transitive triads, whereas cycles were very rare. Moreover, pass-along triads were rare, and double-dominant triads were common in most groups. These patterns did not vary in any systematic way across taxa, study settings (captive or wild) or group size. Two factors significantly affected network motif structure: the proportion of dyads that were observed to interact and the interaction rates of the top-ranked individuals. Thus, study design (i.e. how many interactions were observed) and the behaviour of key individuals in the group could explain much of the variations we see in social hierarchies across animals. Our findings confirm the ubiquity of dominance hierarchies across all animal systems, and demonstrate that network analysis provides new avenues for comparative analyses of social hierarchies.

1. Introduction

Social hierarchies are ubiquitous in human and non-human animal groups [1–4], and such forms of orderliness in societies can have major effects on physiology and fitness of individuals [5–8]. Despite decades of research on the structures of social relations in non-human animals, debate continues about how hierarchies arise from a series of dyadic contests [9–12]. Debate also continues about the ecological and evolutionary origins of social hierarchies—are certain societies uniquely egalitarian or hierarchical, and if so, why [13]?

The study of dominance relations in non-human animals began with the observation that groups of hens often form strictly *linear dominance hierarchies*—a particular form of hierarchy in which all pairs of individuals (dyads) have a dominant–subordinate relation, and all possible relations are transitive (i.e. if A is dominant to B and B is dominant to C, then A is dominant to C) [14,15]. Subsequent empirical studies have tested whether other animal groups are organized into linear hierarchies [16,17], whereas theoretical work has sought mechanistic explanations for why linear hierarchies arise [9,12,18–20]. Nevertheless, perhaps owing to this focus on *linearity* of hierarchies, we have thus far failed to ask a critical question: do dominance hierarchies differ in their structure across animals, and what factors might explain such variation? We bring to bear a large body of work on dominance relations in non-human animals to investigate patterns of variation in hierarchy structure.

Behavioural ecologists have amassed an impressive amount of empirical data on dominance interactions across many animal species under different ecological conditions, providing opportunities to test hypotheses about the causes of social hierarchies. We focus here on several potential causes of variation in hierarchies including group size, evolutionary differences among animal taxa, group stability and the role of key individuals. Group size may affect hierarchy structure for two reasons. First, if the stability of dominance hierarchies

depends on individual recognition [21], then larger groups may be less likely to maintain a stable hierarchy. Second, if dominance relations are the probabilistic outcomes of pre-existing asymmetries in competitive ability (known as the 'prior attributes' model: [22]), increase in group size will decrease the average competitive asymmetry between pairs of individuals, making linear hierarchies less likely [9,23]. In addition to group size, other socioecological differences across species or higher-level taxonomic groups could drive variation in the structure of dominance hierarchies [24]. Moreover, if hierarchies are more likely to arise in stable groups with little change in membership, then we might expect that the structures of dominance relations in groups formed and maintained in captivity might differ from natural groups. The structure of social hierarchies may also be disproportionately influenced by the behaviour of key individuals such as the top-ranked member (i.e. *alpha* individual) [25,26].

A major challenge to comparative studies of dominance datasets is that some aspects of study design could create artefactual correlations with existing measures of hierarchy structure. For example, variations in group size and number of 'null dyads'—unknown relations between pairs of individuals that were not observed to interact—cause bias in the indices of linearity [27]. Variations in observer effort (e.g. the number of interactions observed in a study) can affect the number of null dyads, leading to potentially confounding effects of study design on apparent patterns of hierarchy structure [27]. Past studies have dealt with this problem by 'filling in' null dyads, but doing so also causes biases in linearity measures [27,28]. An alternative measure called hierarchy steepness [29] has been used for a comparative analysis, but this is also sensitive to the presence of null dyads [30]. Recently, we proposed a measure termed 'triangle transitivity', which is based on the proportion of transitive triads among all complete triads (a set of three players in which all pairs have interacted: [27]). While triangle transitivity avoids the pitfalls of filling in null dyads, it simply ignores the triads that contain one or more null dyads, thus providing an incomplete picture of hierarchy structure. What is needed is an analytical approach that allows us to (i) compare hierarchy structure across datasets that differ in the number of group members as well as the frequency of null dyads and (ii) detect patterns that arise in both observed and null dyads. Here, we show that network analysis provides an avenue for such comparisons of dominance relations across vastly different study systems.

Dominance relations can be represented as directed networks termed *dominance networks*, in which nodes, representing individuals, are connected by directed edges pointing from dominant to subordinate individuals [27,31]. Thus, we can apply tools for analysis and comparison of directed networks to understand structural patterns of dominance relations. Here, we use a network method termed *triad census* or *network motif analysis* [32–34], based on the frequencies of triadic configurations, to compare dominance hierarchies from published data. Network motif analysis was developed specifically as a method for comparing the structures of directed networks which vary in numbers of nodes and edges [34], and thus may be suited for comparisons between dominance datasets that vary in group size (network size) and the proportion of dyads that were observed to interact (network density). Motif analysis also allows us to analyse patterns of dominance relations in triads that contain null dyads, for example patterns of triadic relations in which one pair of individuals did *not* interact (figure 1). Thus,
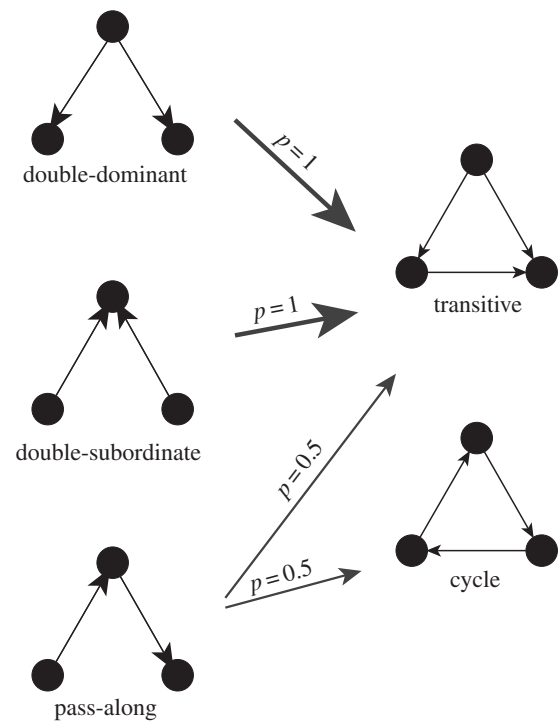

Figure 1. The five connected triads with asymmetric relations. The arrows show the probability, *p*, with which a given two-edge triad becomes a triangle given equal probability of new arrow pointing to the left or right. Double-dominant triads and double-subordinate triads can become transitive only even when the null dyadic relation becomes established. Pass-along triads can become either a transitive or cycle with equal probability.

while traditional measures of hierarchies [9,35] are well suited for analysis of complete directed networks (*tournaments* in network parlance) network motif analysis could provide an alternative approach to analysing dominance data in which some dyads fail to interact. We show that triadic network motifs provide unique insights into the general patterns of dominance hierarchy structure in animals and the processes that give rise to social order. Our overarching goals are twofold: to uncover the general motif structure of dominance relations in non-human animal groups, and to explore whether dominance network structure varies by taxonomy, size or ecology. We show that network motif architecture of dominance hierarchies is surprisingly and consistently orderly across virtually all animal groups. The variations that do exist are influenced primarily by study design (i.e. the number of interactions observed) and the interaction rates of the top-ranked individual in the group.

2. Methods

2.1. Datasets

We gathered published dominance data by searching Web of Science using the keyword 'dominance hierarchy'. We also searched selected journals (*Animal Behaviour*, *Behavioral Ecology*, *Behavioural Processes*, *Behavioral Ecology and Sociobiology*, *Ethology* and *Applied Animal Behaviour Science*) using the same keyword. We added other datasets opportunistically. We included data only from tables that showed raw interaction data. We excluded data on groups of five or fewer individuals and from datasets that observed less than two interactions per individual, because measures of hierarchy are unreliable for such small datasets [27]. If a study observed the same group using the same protocol at different times, we chose the dataset that was collected earlier.

If a study presented data on different behaviours of the same group (e.g. physical aggression and threat displays), we chose the dataset for aggressive encounters. However, if a study included multiple groups that fit the above criteria, we analysed these as separate datasets.

Our total dataset included dominance networks from observations of 172 animal groups extracted from data tables published in 113 studies (electronic supplementary material, table S1). For comparisons of frequencies of two-edge triads (double-dominant, double-subordinate and pass-along: figure 1) against the null model, we excluded 34 datasets for which all dyads had interacted (i.e. there were no null dyads), because two-edge triads cannot exist in randomized complete networks. However, we analysed the relative frequencies of the two types of three-edge triads (transitive and cycle: figure 1) for all 172 networks.

2.2. Empirical triad frequencies

To calculate the triad frequencies, we first converted the raw interaction data (contest matrix) into a matrix of dominance relations (dominance matrix) [31]. In the dominance matrix, the dominant individual received a 1 in its row, and the subordinate received a 0. We used a majority-rule criterion for dominance—for each dyad, we designated the individual that won more than 50% of contests as the dominant. If both individuals won an equal number of contests, then the relation was a tie, and both individuals received a 1 (though this designation matters little here, because ties are rare and were excluded from our analyses). If two individuals were never observed to interact, then they each received a 0. This dominance matrix is directly analogous to an unweighted, directed adjacency matrix from which we can construct a dominance network. In network parlance, a dominant–subordinate relation is an *asymmetric dyad*, a tie is a *mutual dyad*, and two individuals that never interact are a *null dyad*.

For each dominance network, we conducted a *triad census*, which enumerates the frequencies of all 16 possible types of triad configurations, ranging from completely null triads to triads with three mutual dyads [32]. In our study, we considered only the five triad types that consisted of two or three asymmetric edges (figure 1), ignoring mutual edges. Mutual edges were very rare in our empirical data (mean proportion of mutual dyads $\pm$ s.d.: 0.019 ± 0.033), and thus frequencies of triads that include mutual edges were negligible. Triad census was conducted using the *statnet* package in R.

2.3. Null model

The design of the null model is critical for interpreting the results of network motif analysis [33,36]. With respect to this study, there are two behavioural processes that determine the dominance network structure: (i) contests (who engages in interactions with whom), and (ii) wins and losses (given that a pair of individuals interact, who wins?). While both these processes might reflect dominance status, the patterns of contests could also be influenced by multiple factors other than dominance, such as spatial preferences, familiarity and kinship. We did not have information that would allow us to tease apart the contributions of various factors on the patterns of contests in our dominance networks. Thus, we focus here on the effects of the outcomes of contests (wins and losses) on network structure.

We designed our null model to simulate a group in which contests followed the observed patterns, but dominance–subordinate relations were determined randomly. We did this simply by randomizing the direction of each existing edge for a given empirical network. For each network, we generated an ensemble of 1000 simulated networks and calculated a Z-score for the observed frequency of each triadic configuration as $Z = (N_{real} - N_{random})/\text{s.d.}$, where N_{real} was the frequency of that triad in the observed dominance network, N_{random} and s.d. were the mean and standard deviation of the triad frequency in the ensemble of randomized networks.

To confirm the robustness of our results, we also repeated the motif analysis using a different null model in which both the patterns of interactions and the direction of dominant–subordinate relations are randomized ('dyad census-conditioned random graph: [37]). We used this type of null model for previous analyses of triad frequencies [27,31]. Our general results remain the same under this null model, and we present these results in the electronic supplementary material. Our null model also differed from that of some other studies that use randomizations that constrain both in- and out-degree sequences [33,34,38]. We avoid constraining the null model based on in- and out-degrees, because the structure of a dominance hierarchy is defined, in part, by the distribution of out-degrees (i.e. the number of individuals dominated). Thus, constraining the out-degree sequence leads to ensembles of graphs that essentially have the same hierarchical structure and produces uninformative results.

2.4. Significance profiles

Z-scores of triad frequencies can be influenced by sample size—triads that occur more than random in large networks tend to exhibit larger Z-scores than those of small networks. Therefore, following Milo *et al.* [34], we used *significance profiles*, or vectors of normalized Z-scores, to compare the relative patterns of over- and under-abundance of triad frequencies across networks. For each of i triad configurations, we calculated a normalized score as

$$\text{normalized Z-score} = Z_i \left(\sum Z_i^2 \right)^{1/2}. \tag{2.1}$$

Thus, the significance profile reflected the relative significance of triad frequencies rather than reflected the absolute significance. We used normalized Z-scores for comparing dominance structure across animal groups (figure 3).

2.5. Statistical comparisons of significance profiles

To investigate patterns of variation in structures of dominance hierarchies, we computed a correlation coefficient between each pair of significance profiles. Following Stouffer *et al.* [38], we used an uncentred correlation coefficient, r between each pair of significance profiles a and b, defined as

$$r_{a,b} = \sum_{j=1}^{m} \left(\frac{z_{a,j}}{|z_a|} \right) \left(\frac{z_{b,j}}{|z_b|} \right), \tag{2.2}$$

where

$$|z_a| = \sqrt{\sum_{j=1}^{m} (z_{a,j})^2}, \tag{2.3}$$

and j indicates the triad type. The values of r can range from -1 to 1, with negative values indicating negative correlations and positive values indicating positive correlations between the dominance structures of two groups.

We used permutuational MANOVA [39] to test what factors systematically influenced the variation in significance profiles. We used five dependent variables: group size (log-transformed), the proportion of dyads that were observed to interact (i.e. 'network density'; arcsine-square-root-transformed), taxonomic classification, captive/natural status and the relative interaction rates of the top-ranked individual (i.e. *alpha* individual). We identified the alpha individual in each group as the individual with the highest 'David's score', a commonly used index of dominance [40,41]. Interaction rate, I, was calculated as the Z-score of the number of contests an individual engaged in. Thus, for top-ranked individual α, the interaction rate is $I_\alpha = (C_\alpha - \bar{C})/\sigma_C$, where C_α is the number of contests in which alpha individual

was involved, $\overline{C}$ is the average number of contests per individual in the group and σ_C is the standard deviation.

The permutational MANOVA analysis was restricted to the 138 datasets for which there was at least one null dyad. To help balance the sample sizes of different taxonomic groups in our comparisons, we broke up mammalian groups into ecologically and evolutionarily similar groups. Thus, our taxonomic classifications included the following categories: primates ($N = 30$), carnivores ($N = 13$), elephants ($N = 10$), ungulates ($N = 20$), rodents ($N = 3$), marsupials ($N = 3$), birds ($N = 31$), reptiles ($N = 5$), fish ($N = 7$), social insects ($N = 13$) and other invertebrates ($N = 3$). This sample included 54 groups studied in captivity and 84 groups studied under natural conditions. Permutational MANOVA was conducted using the 'adonis' function in the *vegan* package [42].

We used a resampling procedure to confirm that the results of the permutational MANOVA analyses were robust to the effects of pseudo-replication arising from multiple samples of some species. We randomly selected a subset of the data that included only one group per species, and conducted the permutational MANOVA analysis on this reduced dataset. We repeated this procedure 100 times and report the 95% confidence intervals of the test statistics.

Two factors that had significant effects on the correlations between significance profiles—network density and the interaction rates of alpha individuals (I_a). We first determined whether these variables were correlated (and thus violated the assumption of collinearity) using Spearman's rank correlation. We then investigated how I_a and network density correlated with each triad configuration, also with Spearman's rank correlation analysis. This analysis was conducted on the complete dataset as well as randomly sampled subsets (100 replicates) that included one group per species to check for the effects of pseudo-replication, as explained above.

Finally, we conducted a linear aggression to assess how group size and relative observation effort influenced network density. We initially tested a full model with group size (log-transformed), average number of interactions observed per dyad (log-transformed) and their interactions as independent variables and network density (arcsine-square-root-transformed) as the dependent variable. The interaction term was not significant and was dropped from the model.

All statistical analyses were conducted using R v. 3.1.2 [43].

3. Results

The significance profiles reveal clear patterns in the triadic motif structure of dominance networks that are consistent across both taxonomic classification and captive/natural status (figure 2). The patterns of over- and under-representation of triads supported our previous finding that dominance hierarchies are generally transitive [27,31]: in the vast majority of groups, transitive configurations were over-represented (97% of all $N = 172$ groups), and cycles were under-represented (99% of all groups). We also confirmed general patterns for two of the three two-edge triad types [18,31]: pass-along configurations were generally under-represented (89% of $N = 138$ groups with at least one null dyad), and double-dominant triads were commonly over-represented (80% of groups with at least one null dyad). These results were robust to assumptions about the patterns of contests (i.e. who interacts with whom) in the null model (electronic supplementary material). However, there was one clear outlier. A group of captive female Western lowland gorillas [44] exhibited fewer transitive triads and more cycles than expected—a pattern of egalitarianism not seen in any other group (figures 2 and 3). This result shows that departures from the predominant network motif profiles are possible.
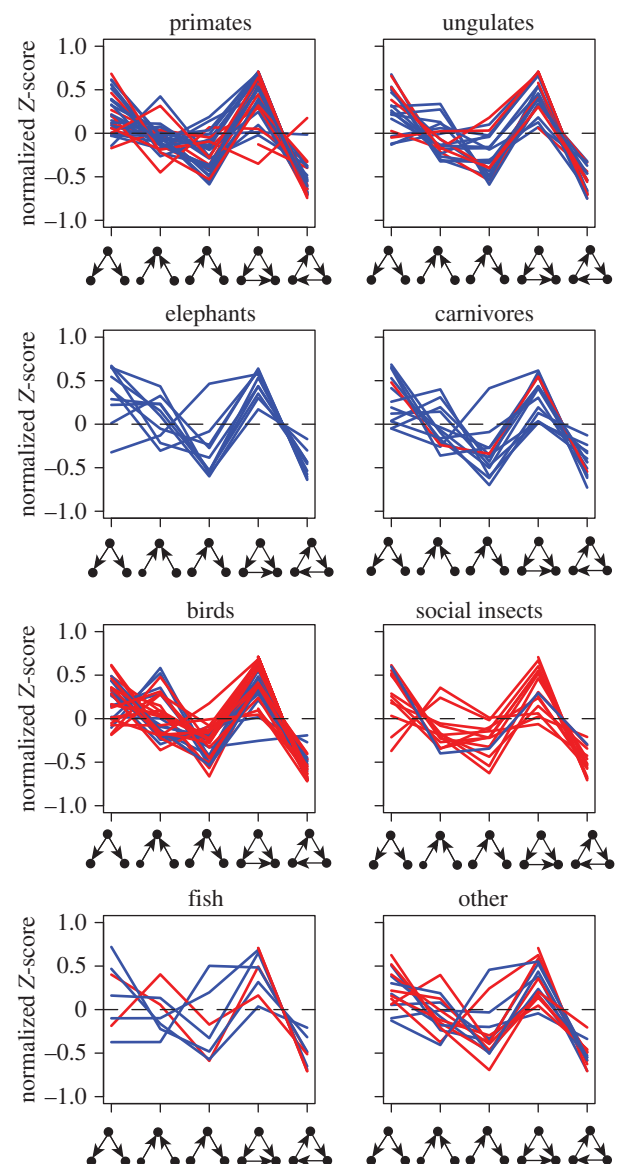

Figure 2. Dominance relations show consistent patterns of triadic motifs across taxonomic groups. The significance profiles for each taxonomic group show the same general pattern of variation. The 'other' group includes rodents, marsupials, reptiles and non-social insects. Blue lines represent studies in animal groups in natural settings, and red lines represent captive groups.

The correlations between significance profiles were generally high (mean $r = 0.70$; median $r = 0.77$), and there was no clear pattern of clustering of high correlations within taxa (figure 3). Neither taxonomy nor captive/natural status of groups explained the variation in significance profiles (table 1). Group size had a marginal effect on the significance profile, but this result was not robust to the effects of pseudo-replication (table 1). The two most significant factors in explaining the variation in significance profiles were the network density (proportion of dyads that interacted) and the interaction rate of the alpha individuals (I_a), and both of these results were robust to the potential effects of pseudo-replication (table 1). Network density and I_a were not correlated with each other (Spearman's $rho = -0.05$, $p = 0.54$).

Increasing network density was associated with decreasing proportions of cyclical triads and increasing proportions pass-along and transitive triads (figure 4 and table 2). Double-dominant triads became less common with increasing network density, but this effect was not apparent after
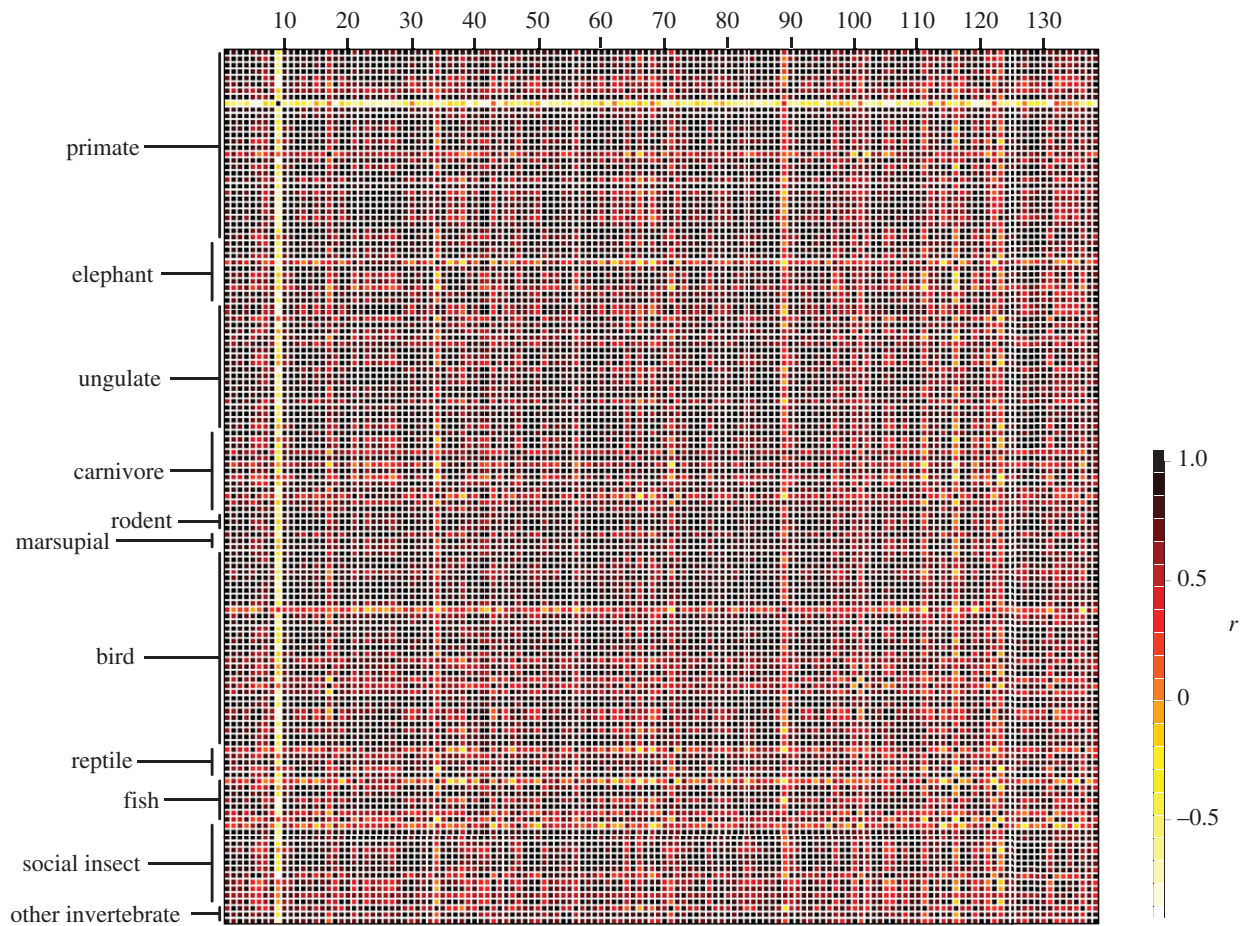
Figure 3. Correlations of significance profiles show that triadic patterns are consistent across taxonomic groups. For a given cell in row a, column b, the colour spectrum represents the correlation coefficient ($r_{a,b}$) between the significance profiles. The rows and columns are organized by taxonomic group, shown on the left. The numbers above correspond to row/column numbers shown in electronic supplementary material, table S1. The 34 groups in which there were no null dyads were excluded, because the full significance profile cannot be calculated in the absence of at least one null dyad. If dominance structures within taxonomic groups resembled each other more closely than those of different groups, then there should be clusters of high correlations along the diagonal. Instead, the colours are fairly uniform across the plot, showing that taxonomic groups do not systematically vary in social structure. One group of lowland gorillas ([44]; row/column 9) showed a highly intransitive dominance structure that caused their triad structure to be negatively correlated with most of the other taxa, producing one light horizontal stripe and one light vertical stripe.

Table 1. Results of permutational MANOVA tests for the effects of group size, network density, captive/natural status, taxonomic classification and interaction rates of alpha individuals (I_α) on variations in significance profiles. p-values shown are Bonferroni-corrected values. In the 'pseudo-replication test', we used a resampling procedure to randomly choose one group for each species and then conducted the permutational MANOVA test on this reduced dataset. This procedure was repeated 100 times, and the means $\pm$ standard errors are shown for all values. In all cases, the analysis excludes groups for which all dyadic pairs have interacted (see Methods). For these tests, the median values are shown, and 95% confidence intervals are reported in parentheses.

|	n	F	partial R^2	p
complete dataset				
group size	138	2.46	0.02	0.07
network density	138	16.96	0.10	<0.001
captive/natural	138	1.21	0.01	0.32
taxonomy	138	0.90	0.06	0.62
I_α	138	9.33	0.06	<0.001
pseudo-replication test: mean $\pm$ s.e.				
group size	67.5 $\pm$ 0.14	2.03 $\pm$ 0.07	0.03 $\pm$ 0.001	0.16 $\pm$ 0.01
network density	67.5 $\pm$ 0.14	8.9 $\pm$ 0.24	0.11 $\pm$ 0.003	0.001 $\pm$ 0.00
captive/natural	67.5 $\pm$ 0.14	1.88 $\pm$ 0.09	0.02 $\pm$ 0.001	0.21 $\pm$ 0.02
taxonomy	67.5 $\pm$ 0.14	0.93 $\pm$ 0.02	0.12 $\pm$ 0.002	0.58 $\pm$ 0.02
I_α	67.5 $\pm$ 0.14	4.35 $\pm$ 0.14	0.05 $\pm$ 0.002	0.02 $\pm$ 0.00
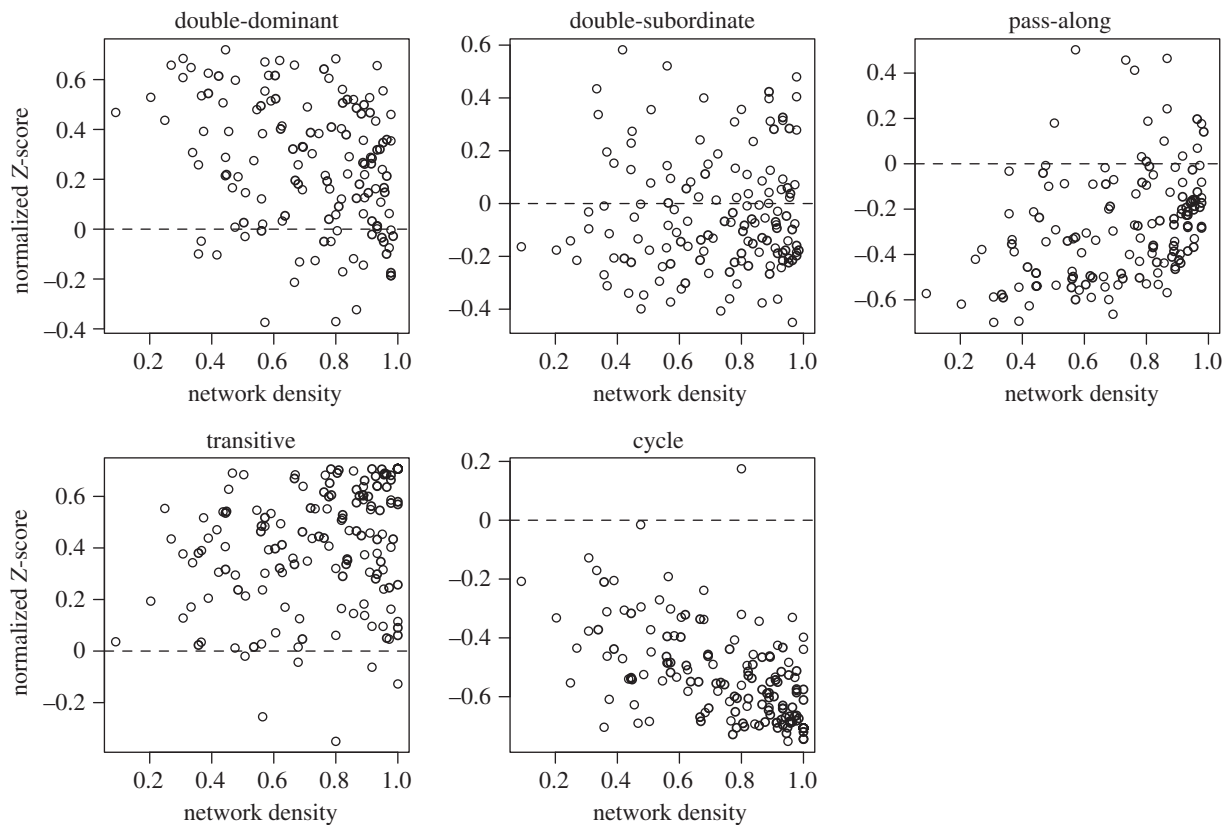
Figure 4. Correlations between network density on triad frequencies. The frequencies of pass-along and transitive triads are positively correlated with network density, whereas the frequencies of double-dominant and cycle triads are negatively correlated with network density. Note that the correlation with double-dominant triads disappear after controlling for pseudo-replication of species in the dataset.

Table 2. Results of Spearman correlation tests for the relationship between network density and triad frequencies. *p*-values shown are Bonferroni-corrected values. 'Complete dataset' and 'pseudo-replication test' as with table 1. In all cases, the sample sizes for double-dominant, double-subordinate and pass-along triads exclude groups in which all dyadic relations are observed because these three triads only exist in incomplete networks.

	n	*rho*	*p**
complete dataset			
double-dominant	138	−0.31	0.001
double-subordinate	138	0.04	1.0
pass-along	138	0.44	<0.001
transitive	172	0.47	<0.001
cycle	172	−0.68	<0.001
pseudo-replication test: mean ± s.e.			
double-dominant	68.4 ± 0.14	−0.27 ± 0.005	0.19 ± 0.02
double-subordinate	68.4 ± 0.14	0.09 ± 0.008	0.91 ± 0.02
pass-along	68.4 ± 0.14	0.46 ± 0.005	0.002 ± 0.001
transitive	84 ± 0	0.40 ± 0.004	0.003 ± 0.001
cycle	84 ± 0	−0.65 ± 0.004	0.000 ± 0.000

controlling for pseudo-replication (figure 4 and table 2). In effect, increasing network density diminished some of the prevailing patterns of two-edge triads (i.e. excess of double-dominant and rarity of pass-along) and strengthened the prevailing patterns of three-edge triads (excess of transitive and rarity of cycle). In turn, patterns of network density were predicted by both relative observation effort ($t_{136} = 12.9$, partial $R^2 = 0.50$, $p < 0.001$) and group size ($t_{136} = -2.5$, partial $R^2 = 0.02$, $p = 0.01$), and together they explained a majority of the variation in network density (electronic supplementary material, figure S1; full model: $F_{2,136} = 102.6$, $R^2 = 0.59$, $p < 0.001$). These findings align with previous studies showing that double-dominant configurations are common and pass-along configurations are rare during the early stages of hierarchy formation [45], and studies may pick up different patterns of hierarchy structure based on how many interactions were observed by researchers.

The interaction rates of the top individuals were also related to the frequencies of certain triad configurations. I_α was positively correlated with relative frequency of the
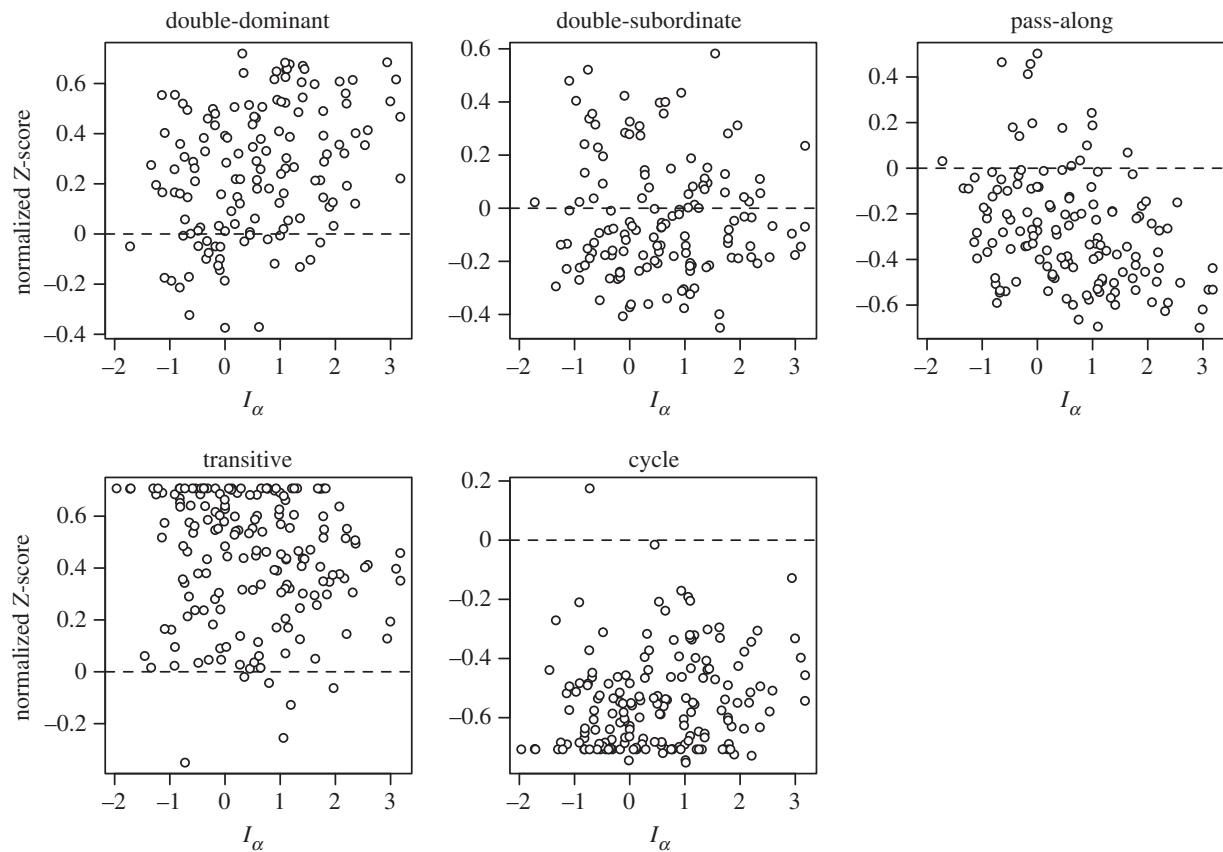
Figure 5. Correlations between the interaction rate of the top-ranked individual (I_α) and triad frequencies. The frequencies of double-dominant triads are positively related to the propensity for top-ranked individuals to engage in more contests. Conversely, there are fewer pass-along triads in groups where top individuals engage in more contests.

Table 3. Results of Spearman correlation tests for the relationship between the interaction rate of alpha individuals (I_α) and triad frequencies. p-values shown are Bonferroni-corrected values. 'Complete dataset' and 'pseudo-replication test' as with table 1. In all cases, the sample sizes for double-dominant, double-subordinate and pass-along triads exclude groups in which all dyadic relations are observed because these three triads only exist in incomplete networks.

	n	rho	p*
complete dataset			
double-dominant	138	0.35	<0.001
double-subordinate	138	−0.004	1.0
pass-along	138	−0.35	<0.001
transitive	172	−0.17	0.11
cycle	172	0.18	0.08
pseudo-replication test: mean ± s.e.			
double-dominant	68.4 ± 0.14	0.35 ± 0.006	0.03 ± 0.005
double-subordinate	68.4 ± 0.14	−0.05 ± 0.007	0.99 ± 0.01
pass-along	68.4 ± 0.14	−0.33 ± 0.005	0.05 ± 0.003
transitive	84 ± 0	−0.18 ± 0.005	0.51 ± 0.01
cycle	84 ± 0	0.21 ± 0.005	0.36 ± 0.01

double-dominant triads and negatively correlated with the relative frequency of pass-along triads (figure 5 and table 3).

4. Discussion

Our comparisons of triad motifs across dominance networks revealed general patterns in the structures of dominance hierarchies across virtually all animals. In the vast majority of groups we analysed, transitive triads were more abundant than expected, whereas cycle triads were relatively rare. There was also a general over-abundance of double-dominant triads and under-abundance of pass-along triads.

We identified two factors that influenced the variation in triad motif patterns in dominance networks. First, increasing network density—i.e. the proportion of dyads for which the

dominant–subordinate relation could be inferred—was associated with increases in the prevailing patterns of complete triads (transitives become more common and cycles become more rare) and an increase in the frequency of pass-along triads. This may reflect a limitation of applying network motif analysis to highly dense networks—when networks are very dense, there are few incomplete triads (three nodes with less than three edges), and this could constrain the possible conformations of randomized networks. Thus, patterns of two-edge triads could diminish, whereas patterns of complete triads become magnified. In turn, half of the variation in network density was explained by relative observation effort (i.e. the average number of interactions observed per dyad). Thus, some of the apparent differences in dominance hierarchy structure across animals may be a consequence of the study design: e.g. how many animals to observe and how much interaction data to collect. Including network density as a covariate in our analysis was important for teasing apart the artefactual and biological sources of variation in dominance hierarchies.

Despite the potential confounding effects of network density, we were able to detect a significant effect of the behaviour of top-ranked individuals (alpha individuals) on dominance hierarchy structure. In groups where alpha individuals engaged in more contests, there were more double-dominant triads and fewer pass-along triads. As the interaction rate of the alpha individual increases relative to the other members, double-dominant triads may become more frequent, because two subordinates are not more likely to interact (i.e. A dominates B and C, but B and C are not more likely to interact: figure 1). Similarly, pass-along triads may become less frequent because they become transitive triads (i.e. A interacts with, and dominates, C: figure 1). These results support the idea that key individuals may have disproportionate influence on dominance hierarchies [25,46], and suggest that the presence of such 'keystone individuals' may be a prominent source of variations in dominance hierarchies across all types of animal groups.

Our analysis shows that the structure of dominance hierarchies is not influenced by captivity—a striking result that suggests that artificial ecological conditions may not fundamentally alter the social dynamics that give rise to social hierarchies. We also did not detect quantitative differences among taxonomic groups in the structure of dominance hierarchies; a surprising result considering that these are groups with clear qualitative differences in ecology, cognitive capacity and sociality. Our results do not necessarily show that ecology and evolution do not matter in hierarchy formation. Rather, we suggest that social dynamics that are important in shaping hierarchy structure—e.g. the propensity of dominant individuals to engage in more contests—are common across animals of most taxonomic groups and in captive and natural settings.

We also showed that group size had little effect on the network motif structure of dominance hierarchies. This finding supports our previous assertion that group size does not affect the transitivity of dominance relations [27]. In the previous study, we showed that a negative correlation exists between group size and the linearity index [17], but this is an artefact of the data imputation routine (i.e. randomly filling in unknown data) used to calculate this index [27,28]. The imputation procedure introduces more bias towards intransitivity with increasing sparseness (the frequency of unknown dyads), and larger dominance networks tend to be more sparse [17]. The network motif method provides a more accurate basis for comparison of hierarchy structure because it avoids the pitfalls of filling in unknown data.

Group size has been thought to play an important role in the formation of dominance hierarchies for at least two reasons. First, group size could affect the capacity for individual recognition, which, if present, could stabilize dominance hierarchies [21,47]. Second, if dominance relations are decided by relative differences in competitive ability (resource holding potential), then larger groups should have less stable hierarchies, because the average difference between group members become small [4,19,48]. In fact, early theoretical work found that, for any realistic group size, dominance relations settled simply by pre-existing competitive asymmetries could produce linear hierarchies only under very stringent conditions that are rarely met (e.g. only when very slight differences in competitive ability perfectly predict dominance relations) [9]. The current paradigm is that other social mechanisms such as winner and loser effects and third-party effects (bystander effects) all play some role in the emergence of dominance hierarchies [10,12,20,49,50]. Our finding that the interaction rate of alpha individuals influences dominance structure, could be a reflection of how winner effects influences variations in hierarchy structure.

An important missing piece in our analysis is the temporal component of hierarchy formation and maintenance—how do the sequence of dominance interactions help structure hierarchies, and does this process vary across groups [18,51]? The over-abundance of double-dominant triads and under-abundance of pass-along triads align with an influential model of the sequential process of hierarchy formation. In a series of studies on hens and sparrows, Chase and co-workers [36,51] found that double-dominant triads are over-represented, and pass-along triads are under-represented in the early stages of hierarchy formation. These biased patterns of two-edge triad motifs have important implications for the final dominance hierarchy structure. If reversals in dominance relations are rare, cycles arise only from pass-along triads and double-dominant triads inevitably become transitive (figure 1; [18,31,51]). Thus, the dearth of pass-along triads and abundance of double-dominant triads in early sequences of interactions could make the resulting social structure more likely to become completely transitive. This process suggests that orderliness may be well established before the complete set of interactions has occurred, i.e. while the interaction network is still very sparse [18,52]. Because published studies rarely provide the raw temporal sequence of contests, we could not explore the ontogeny of the dominance networks in our sample. However, this sequential information should be available for most datasets: researchers will almost inevitably record the time-ordered sequence of dominance interactions. We echo previous suggestions that temporal analysis of network dynamics could provide new avenues for comparisons of social processes across animal groups [53,54].

The social processes involved in animal contests have been of interest to evolutionary biologists for some time [3,55,56]. Despite the importance of dominance hierarchies to the theories of social evolution, this study is one of few comparative studies to look for general patterns across many species. We suggest that effectively linking theory to empirical data requires a multi-dimensional view of social structure that incorporates the dynamics of unobserved or unobservable social interactions [27,28], as well as the temporal dynamics of how hierarchies emerge [18]. Network

theory, and network motif analysis in particular, provide useful tools for such endeavours. Network motifs have been widely used for analyses of large directed networks, including biological, technological and sociological systems, and have been particularly useful for identifying repeated organizational patterns in complex systems [34,57,58]. Animal social networks with directed relations such as dominance networks and information processing networks [59] provide new perspectives on the organization of complex systems. Because they are amenable to experimental and comparative studies, animal social systems will help us understand how order and organization emerge across the spectrum from the simplest of social groups to the most complex of societies.

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