Received: 17 July 2024 | Accepted: 24 September 2024

DOI: 10.1111/1365-2656.14203

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Hierarchies inferred from different agonistic behaviours are not always comparable

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Funding information
Max Planck Society

Handling Editor: Eric Vander Wal

Abstract

1. Social hierarchies are widely used to predict life-history patterns and priority of access to resources. Yet, behavioural ecology and social sciences lack a consistent relationship between specific behaviours and social rank across studies.
2. I used published data sets from 42 groups of 25 species representing several taxa to determine whether hierarchies inferred from different behaviours are similar or (in)consistently different at both individual and group levels.
3. Ranks inferred from yielding interactions in the absence of aggression ('ritualized') were often comparable to ranks inferred from decided aggression (unambiguous outcome) but not to ranks inferred from undecided aggression. Accordingly, hierarchies inferred from data sets including only decided interactions were steeper than those inferred from data sets including undecided aggression.
4. These results support the hypothesis that aggression can be context-dependent and might reflect less stable or mutually recognized relationships than (ritualized) yielding interactions.
5. I discuss the consequences of choosing different behaviours to infer social hierarchies and the difficulty of making generalizations from one species or taxon to another. Finally, I recommend that the use of ritualized yielding and certainly the use of decided over undecided interactions to infer social hierarchies should be preferred, especially in comparative studies which go beyond taxon-specific idiosyncrasies.

KEYWORDS
aggression, dominance, social hierarchy, social rank, steepness, submission/yielding

1 | INTRODUCTION

Social rank can determine priority of access to food (Ekman & Lilliendahl, 1993) and mates (Dubuc et al., 2011), ultimately influencing survival (Lahti, 1998) and reproductive success (Fedigan, 1983). Consequently, the concept of social rank has a pivotal role in studies of behavioural ecology and social sciences (Strauss, Curley, et al., 2022). While various studies introduce (de Vries, 1998; Douglas et al., 2017; Neumann et al., 2011), optimize (Goffe et al., 2018; Newton-Fisher, 2017; Schmid & de Vries, 2013), criticize or compare (Neumann et al., 2011, 2018; Vilette et al., 2020) different techniques for reliably inferring social ranks, they often draw increased attention to these techniques, potentially overlooking the biological significance of the nature of interactions used to infer social ranks

(Strayer & Strayer, 1976). For example, empirical studies may use more than one technique to verify the robustness of an inferred hierarchical structure (Hewitt et al., 2009; Smit et al., 2022), but they may not explore how the inclusion/exclusion of different behaviours can impact this structure. In this study, I use data from species of several taxa to ascertain if social hierarchies inferred from different behavioural data sets are consistently or inconsistently different, as previously speculated (Bernstein, 1981; Lewis, 2002; Rowell, 1974), at both individual (rank) and group (hierarchy) levels.

Most studies use aggressive and/or yielding ('submission'; Table 1c) interactions in the absence of aggression to infer social hierarchies. Both aggression and yielding can be observed within a social group, but they likely represent different perspectives of (agonistic) social relationships rather than the opposite ends of a behavioural continuum (McCormick & Holekamp, 2022). The expression of aggression is often subject to context, individual incentives (Bernstein, 1981) or personality (Briffa & Weiss, 2010) and might not reflect hierarchical relationships. It can increase with hunger (Janson & Vogel, 2006), in the presence of food or mates (Cafazzo et al., 2010; Smit, under review), when protecting an offspring (Maestripieri, 1994) or it might depend on coalitionary support (Perry, 1996) or group size (Smit & Robbins, 2024). The value of a resource in relation to the cost for acquiring it or the probability to do so might also influence aggression, and thus, the direction of aggression between two individuals might depend on the disputed resource (e.g. mates vs. food; Hand, 1986; Matsumura & Kobayashi, 1998) or the presence of it (Bonanni et al., 2007). Particularly intersexual aggression might not be a reliable proxy of hierarchical relationships if females are generally less (Campbell, 2013; or more: McCormick & Holekamp, 2022) aggressive than males, manifest their dominance through non-aggressive means (Kappeler et al., 2022), respond submissively to aggression more often (Vervaecke et al., 2000) or have a lower tolerance of physical risk (Campbell, 2013). Hence, females may appear to outrank fewer males in hierarchies inferred from aggression than in hierarchies inferred from yielding in the absence of aggression ('ritualized'; Table 1c; de Waal, 1989; Lewis et al., 2022; Noë et al., 1980).

Aggressive interactions might fail to reflect hierarchical relationships even irrespective of context or group composition. When an individual directs aggression to another and the latter ignores it or does not yield, the interaction might not reflect a mutually acknowledged hierarchical relationship. Studies which take into account such 'undecided' interactions, that is, interactions where none or both individuals yield (Hausfater, 1975; Pereira & Kappeler, 1997), consider 'winners' (Table 1d) those who initiate the interactions (Diniz et al., 2019; Hewitt et al., 2009; Satoh & Ohkawara, 2008). Initiation might indeed occasionally influence winning probability (Lewis et al., 2022), but an individual might 'win' regardless of whether it initiated the interaction, as long as

TABLE 1 Glossary.

(a) Avoidance	*B* leaves its spatial position in response to *A*'s movement, but *A* does not occupy *B*'s position (Marler, 1955)
(b) Supplant/displacement	*B* leaves its spatial position in response to *A*'s movement and *A* occupies *B*'s position (Whitten, 1983). In birds, supplants are often considered intentional (Tarvin & Woolfenden, 1997), but in mammals, it is often difficult to determine if *A* was provoked to occupy the position of *B* from *B*'s movement (see Tilson & Hamilton, 1984) for an exception)
(c) Yielding	*B* avoids or is supplanted by *A* (see *a* and *b* above). The interaction is termed 'ritualized' if it occurs in the absence of *A*'s aggression; see also 'formal dominance' (de Waal, 1989). I use the term 'yielding' because in contrast to the commonly used term 'submissive' (or 'dominant'; Koenig, 2002; Trisko & Smuts, 2015), it does not imply a function (Watts, 2010)
(d) Winner/loser	*B* is considered the loser and *A* the winner in interactions where *B* yields to *A*, regardless if *B* yielded in response to aggression from *A* or not; but only if *A* did not yield to *B* too
(e) Aggression	*A* threatens or physically hits *B*
(f) Decided interaction	It can involve aggression from none, one or both sides but yielding only from one (unambiguous outcome). 'Initiated aggression' (Figure 1) includes both decided and undecided aggression
(g) Steepness	A measure of the overall competitive asymmetries among a group's members. The steepness of a social hierarchy is usually measured as the slope of the regression line between the inferred cardinal ranks (i.e. 1, 2, 3...) and rank scores (e.g. Elo or David's scores) of a group of individuals. Larger differences in rank scores produce steeper slopes. It varies from 0 to 1

it does not yield but its opponent does (Solberg & Ringsby, 1997). Therefore, yielding behaviours likely reflect clearer interaction outcomes (Langbein & Puppe, 2004) and might be more consistent ('unidirectional'; Cafazzo et al., 2010; Trisko & Smuts, 2015) than aggressive interactions, ultimately inferring more reliable and steep social hierarchies (Table 1g).

Despite the influence of the behavioural data set on the emerging structure of an inferred social hierarchy (Bonanni et al., 2007; Robbins, 2008), there is no consistent relationship between specific behaviours and social rank across studies (Clutton-Brock & Janson, 2012; Langbein & Puppe, 2004; Lehner, 1998). Some studies combine aggressive with ritualized yielding interactions (Shargal et al., 2008; Sharpe et al., 2013; Zhang et al., 2018)—sometimes showing inconsistency even within species (Brown, 1963). Some of these studies have used unconventional combinations of behaviours, for example, combining ritualized yielding and undecided aggression but excluding decided aggression (Clutton-Brock et al., 1976; Fairbanks, 1994) or combing several behaviours excluding ritualized yielding (Bruinzeel et al., 2006; Silk et al., 1981). Finally, certain studies have used aggressive interactions as a substitute where yielding interactions cannot be recorded or they are rare (Jaffe & Isbell, 2010; Lodwick, 2014; see 'Relevant literature' in the Supporting Information for more examples).

Understanding how the use of different behavioural data sets can influence the emergent structure of the inferred social hierarchies can make estimations of the social structure more robust and elucidate previously unknown aspects of social life that determine social behaviour and fitness (Davies et al., 2012). Additionally, it can inform studies on humans and other species, where although hierarchical relationships can form without aggression (Burgoon et al., 1998; Burgoon & Dunbar, 2006), aggression is often used as a proxy of dominance (Zeng et al., 2022). In this article, I aimed to compare the properties of social hierarchies inferred from five different behavioural data sets: (i) ritualized yielding, that is, yielding in the absence of aggression; (ii) all yielding, that is, yielding in the absence or in response to aggression; (iii) initiated aggression, that is, aggression followed or not by yielding; (iv) decided aggression, that is, aggression followed by yielding and (v) undecided aggression, that is, aggression not followed by yielding (Figure 1; Table 1). I inferred 105 hierarchies of 42 groups of 25 species aiming to detect any species- or taxon-specific patterns. At the individual level, I tested if the assignment of social rank is sensitive to the data set used to infer the social hierarchy. First, since aggressive interactions can be condition and time dependent with winners/losers depending on the context, I predicted that individual ranks inferred from aggressive interactions are different to ranks inferred from yielding interactions. Second, I predicted that individual ranks inferred from different data sets including exclusively decided interactions are similar among them but different to ranks inferred from data sets including undecided interactions—which can have more inconsistent 'outcomes'. At the group level, I tested if hierarchies inferred from ritualized yielding interactions are steeper (show greater despotism) than hierarchies inferred from all yielding, which are, in turn, steeper than hierarchies inferred from decided, initiated and undecided aggressive interactions.

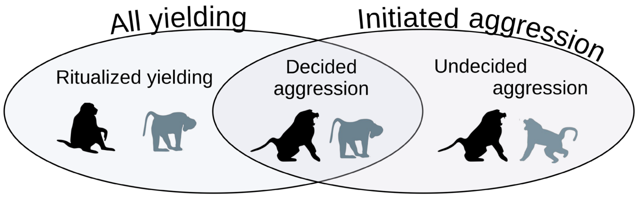


FIGURE 1 Behaviours used to infer social hierarchies. The left ellipse includes all yielding behaviours. The right ellipse includes all aggressive behaviours ('initiated aggression'). The intersection of the two ellipses includes only yielding in response to aggression ('decided aggression'). 'Winners' in black (left) and 'losers' in blue (right).

2 | METHODS

2.1 | Data collection

In early 2023, I conducted a non-systematic literature search in a widely used academic search engine using the key word combinations: (dominance OR hierarchy OR agonism OR matrix) AND (aggression OR submission). After each search, I checked the titles, abstracts and, if relevant, main texts of the articles on the first page (10 articles) as automatically sorted to identify studies that provided at least two relevant matrices for the same group or set of individuals over the same data collection period. When the last three results on a page included a relevant article, I continued checking the articles on the next page. Additionally, I searched for relevant studies in published collections of matrices (Neumann & Fischer, 2023; Shizuka & McDonald, 2015; Strauss, Curley, et al., 2022; Strauss, DeCasien, et al., 2022). I extracted the matrices from the relevant papers and if needed I transposed them in order to fit a consistent format with 'winners' on rows and 'losers' on columns. 'Winners' and 'losers' were specified in the original studies.

I aimed to collect interaction matrices from different taxa as well as both intra- and intersexual (see Table S1 for details) matrices to obtain the most general results possible. I retained only matrices with at least five individuals (average number of individuals± S.D.: 11.2 ± 6.54) and less than 50% of unknown relationships (Neumann & Fischer, 2023). When two individuals were never observed interacting, I considered their relationships unknown. In the retained matrices, the average number of interactions per individual was 35 ± 29 (±S.D.): 32 ± 27 for ritualized yielding, 46 ± 35 for all yielding, 35 ± 24 for initiated aggression, 27 ± 26 for decided aggression and 19 ± 15 for undecided aggression.

From the collected matrices, 12 included all yielding interactions and in 17 cases I obtained an all yielding matrix by adding the provided decided aggression and ritualized yielding matrices (Figure 1). Overall, in my analyses, I used 23 ritualized yielding, 29 all yielding, 27 initiated aggression, 22 decided aggression and 4 undecided aggression matrices from 42 groups of 25 species (Table 2 and Table S1; Original studies: Bartlett & Meier, 1971; Bonanni et al., 2007; Cheney, 1977; Duboscq et al., 2013; Grunau & Kuester, 2001; Ito, 1993; Jenks et al., 1995; Kappeler et al., 2022; Kaufman, 1994; Lemasson et al., 2006; Loy et al., 1993; Loy & Harnois, 1988; Lu et al., 2008; Moore, 1978; Nelissen, 1985; Norscia & Palagi, 2015; Overdorff et al., 2005; Rhine, 1972; Sapolsky, 1983; Setchell & Dixson, 2001; Seyfarth, 1976; Silk et al., 2019; Tilson et al., 1988; Vervaecke et al., 2000; Wickings & Dixson, 1992; Woolfenden & Fitzpatrick, 1977).

2.2 | Social rank and steepness

I used the function *elo_steepness_from_matrix* from the package *EloSteepness* (Neumann & Fischer, 2023) to calculate individual ranks and steepness of the social hierarchy for each matrix. Individual ranks corresponded to the cumulative winning probability, that is, the sum of the probabilities for each individual to 'win' an interaction against another from its group. I standardized the winning probabilities per group and matrix such that the highest score was 1 and the lowest score was 0. This score-based metric reflects rank asymmetries more accurately than metrics that provide equidistant ranks (1,2,3…). Additionally, steepness calculated with this recently developed Bayesian method based on Elo rating (Neumann et al., 2011) shows lower dependence on the percentage of unknown relationships than earlier methods in which sparser data sets produced lower steepness (Neumann & Fischer, 2023). Nonetheless, to verify my results, I reran my analyses using David's scores (David, 1987) which have been commonly used in static, matrix-based, approaches.

In all study species, at least one of the inferred hierarchies had a mean steepness value larger than 0.7. The only exception was Guerezas, for which the maximum mean steepness value was 0.46. Therefore, the species in the data set appear to form relatively structured social hierarchies, and thus, the inference of such hierarchies is biologically justified.

2.3 | Phylogeny

I generated a consensus phylogeny for the mammals in the data set. In two cases, I used a close relative: *Canis lupus* instead of *Canis familiaris* and *Equus caballus* instead of *Equus przewalskii*. I downloaded a credible set of 1000 trees of mammalian phylogenetic history from vertlife.org/phylosubsets/ (February 2024). I used R package *ape* (Paradis & Schliep, 2019) to find the consensus tree (function *consensus*), compute the branch lengths (function *compute.brlen*) and convert the tree into a covariance matrix that reflects the shared phylogenetic history among all species pairs in the data set (function *vcv.phylo*).

2.4 | Statistical analysis

2.4.1 | Individual rank assignment

To determine if different behavioural data sets infer consistently different/similar ranks, I calculated a correlation coefficient between the standardized individual ranks inferred using the different matrices. Given that different groups of the same species can show differences in the properties of their hierarchies (e.g. Kappeler et al., 2022), dominance relationships are likely not strictly species-specific. Therefore, I compared only matrices of the same group over the same period of time. Specifically, I ran one test per matrix pair (i.e., two matrices from the same group including different behaviours collected over the same period of time) to (i) avoid assumptions that the described relationships exist in all groups/species, (ii) ensure that the reported correlations are not a result of between-group/species variation and (iii) detect potential inconsistencies among groups or species. Notably, this analysis did not take into account the number of individuals, which might influence the correlation of ranks inferred from different data sets.

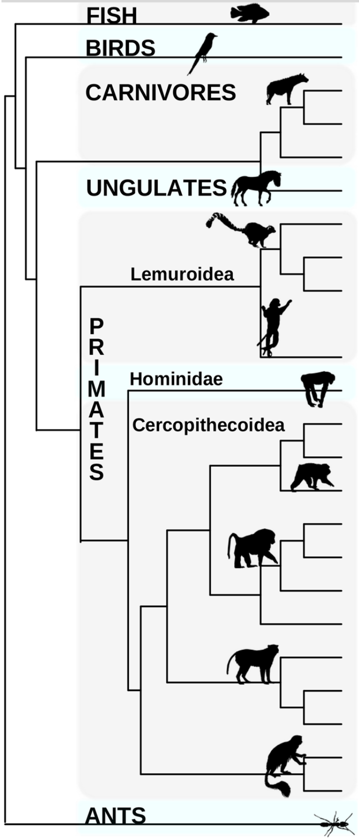
2.4.2 | Interaction distribution

To determine if the numbers of different kinds of interactions between individuals are similar, I calculated a correlation coefficient between dyadic numbers of interactions in each matrix pair. Specifically, I transformed each matrix into a vector and I calculated the correlation coefficient for each pair of vectors. Note that in each vector, two entries corresponded to each dyad of individuals (one with the 'wins' of A over B and one with the 'wins' of B over A). Before each correlation test, I removed the elements of the vectors that corresponded to the diagonal elements of the source matrices because they are always equal to zero (they represent the number of interactions of an individual with itself) and could bias the estimation of the correlation coefficient. Notably, this analysis did not take into account individual observation times, which can influence observed interaction quantity.

2.4.3 | Steepness

To determine if data sets including only decided interactions infer consistently steeper hierarchies than data sets including undecided interactions, I ran a general linear mixed model (GLMM) with beta error structure, response variable the mean steepness of a given hierarchy (extracted from the posterior steepness distribution; ranging from 0 to 1) and main explanatory variable the behavioural data set used to infer the hierarchy. I also fitted the number of individuals and the mean number of interactions per individual (Neumann et al., 2018; Neumann & Fischer, 2023) as fixed factors and the study and species as random factors. I did not transform the response variable as recommended for models using a beta error distribution because all values were larger than zero. Then, I also ran a

TABLE 2 Confidence of the rank correlation tests.



Species	Groups	RY-AY	RY-IA	RY-DA	RY-UA	AY-IA	AY-DA	AY-UA	IA-DA	IA-UA	DA-UA
Auratus cichlids	1	–	–	–	–	1 (1)	–	–	–	–	–
Florida scrub jays	1	–	–	–	–	–	0.92 (1)	–	–	–	–
Feral domestic cats	1	–	–	–	–	1 (1)	–	–	–	–	–
Spotted hyaenas	1	–	–	–	–	0.95 (1)	–	–	–	–	–
Dogs	1	–	–	–	–	1 (1)	–	–	–	–	–
Przewalski horses	1	–	0.89 (1)	–	–	–	–	–	–	–	–
B&W Ruffed Lemurs	1	–	–	–	–	0.83 (0.84)	–	–	–	–	–
Ring-tailed lemurs	2	1 (1)	–	1 (1)	–	–	1 (1)	–	–	–	–
Common brown lemurs	1	–	–	–	–	1 (1)	–	–	–	–	–
Collared brown lemurs	1	–	–	–	–	–	1 (1)	–	–	–	–
Verreaux's sifakas	2	1 (1)	–	0.89 (1)	–	–	1 (1)	–	–	–	–
Bonobos	2	0.81 (1)	0.71 (1)	0.64 (0.99)	0.25 (0.49)	0.48 (0.98)	0.92 (1)	0.22 (0.63)	0.73 (0.98)	0.71 (0.89)	0.39 (0.48)
Rhesus macaques	1	1 (1)	–	1 (1)	–	–	1 (1)	–	–	–	–
Stumptail macaques	2	–	–	–	–	0.93 (1)	–	–	–	–	–
Crested macaques	2	1 (1)	1 (1)	1 (1)	–	1 (1)	1 (1)	–	1 (1)	–	–
Olive baboons	3	1 (1)	–	–	–	1 (1)	–	–	–	–	–
Chacma baboons	3	–	–	–	–	–	–	–	1 (1)	–	–
Yellow baboons	3	–	1 (0.98)	–	–	–	–	–	–	–	–
Mandrills	3	0.96 (1)	0.46 (0.97)	0.87 (1)	0.16 (0.68)	0.49 (0.98)	0.95 (1)	0.16 (0.71)	0.52 (0.97)	0.46 (1)	0 (0.66)
Patas monkeys	3	0.96 (1)	–	0.89 (1)	–	–	0.98 (1)	–	–	–	–
Vervet monkeys	1	–	–	–	–	–	–	–	1 (1)	–	–
Campbell's monkeys	1	–	0.78 (1)	–	–	–	–	–	–	–	–
Guerezas	1	–	0.27 (0.86)	–	–	–	–	–	–	–	–
Hanuman langurs	2	–	1 (1)	–	–	–	–	–	–	–	–
Ponerinae	2	–	–	–	–	–	0.99 (1)	–	–	–	–
Average		0.97 (1)	0.76 (0.98)	0.9 (1)	0.21 (0.58)	0.88 (0.98)	0.98 (1)	0.19 (0.67)	0.85 (0.99)	0.58 (0.95)	0.2 (0.57)

Note: Each cell contains the average proportion of posterior draws above zero for the correlation test between ranks inferred from the column data sets. Numbers in parentheses correspond to the confidence of the correlation tests of dyadic interactions.

Abbreviations: AY, all yielding; DA, decided aggression; Groups, number of groups; IA, initiated aggression; RY, ritualized yielding; UA, undecided aggression.

phylogenetically controlled version of the model including only the mean steepness values of hierarchies of mammals, to examine the impact phylogeny on my results. Finally, to test if the uncertainty of steepness is greater in hierarchies based on (undecided) aggressive interactions, I ran a similar model to the above, this time using as a response variable the uncertainty of the steepness calculation, that is, the length of the 89% credible interval corresponding to the difference of the maximum and minimum steepness value provided by the 89% of the posterior samples.

I used R version 4.1.2 to run the above analyses. I calculated correlation coefficients with a Bayesian statistical test (function *correlationBF* from R package *BayesFactor*; Morey et al., 2024). I fitted the GLMMs with Hamilton Markov chains, using function *brm* from R package *brms* (Bürkner, 2017). I used informative priors (normal (0,1) for all continuous variables) and four chains with 2000 iterations in each. All $\hat{R}$ values were ≤1.01, indicating model convergence.

3 | RESULTS

I present here the results based on Elo-rating; the results based on David's score were qualitatively similar (Tables S2 and S3).

3.1 | Individual rank assignment and interaction distribution

3.1.1 | Differences among different data sets of decided interactions

Individual ranks inferred from ritualized yielding were always positively correlated with ranks inferred from all yielding (mean rho ± S.D.: 0.76 ± 0.25) and decided aggression (0.61 ± 0.31; Figure 2a: rows RY-AY and RY-DA). Accordingly, individual ranks inferred from all yielding interactions were always positively correlated with ranks inferred from decided aggression, with an average correlation coefficient of 0.74 ± 0.22 (Figure 1a; rows AY-DA). The average confidence (posterior draws above zero) of these positive correlations was ≥90% (Table 2: columns RY-AY, RY-DA and AY-DA). The number of dyadic ritualized yielding interactions was strongly positively correlated with the number of interactions of all yielding (mean rho ± S.D.:0.83 ± 0.18; confidence: 100%) and decided aggression (0.58 ± 0.16; 90%). Accordingly, the number of all yielding interactions was positively correlated with the number of decided aggressive interactions (0.81 ± 0.16; 98%; Table 2: columns RY-AY, RY-DA and AY-DA, values in parentheses).

3.1.2 | Decided versus undecided interactions

Individual ranks inferred from undecided aggression were always negatively correlated with ranks inferred from ritualized yielding (mean rho ± S.D.: −0.26 ± 0.09; confidence: 79%), all yielding (−0.30 ± 0.11; 81%) or decided aggression (−0.32 ± 0.34; 80%; Figure 2a and Table 2: rows/columns RY-UA, AY-UA and DA-UA; see also Figure 2b for an example). For the negative correlations, the confidence corresponds to the posterior draws below (instead of above) zero. The number of dyadic undecided aggression interactions was essentially not correlated with the number of interactions of ritualized yielding (mean rho ± S.D.: 0.04 ± 0.06; range: −0.07 to 0.19; confidence: 58%), all yielding (mean rho ± S.D.: 0.08 ± 0.03; confidence: 67%) and decided aggression (0.04 ± 0.07; 57%; 2: columns RY-UA, AY-UA and DA-UA, values in parentheses).

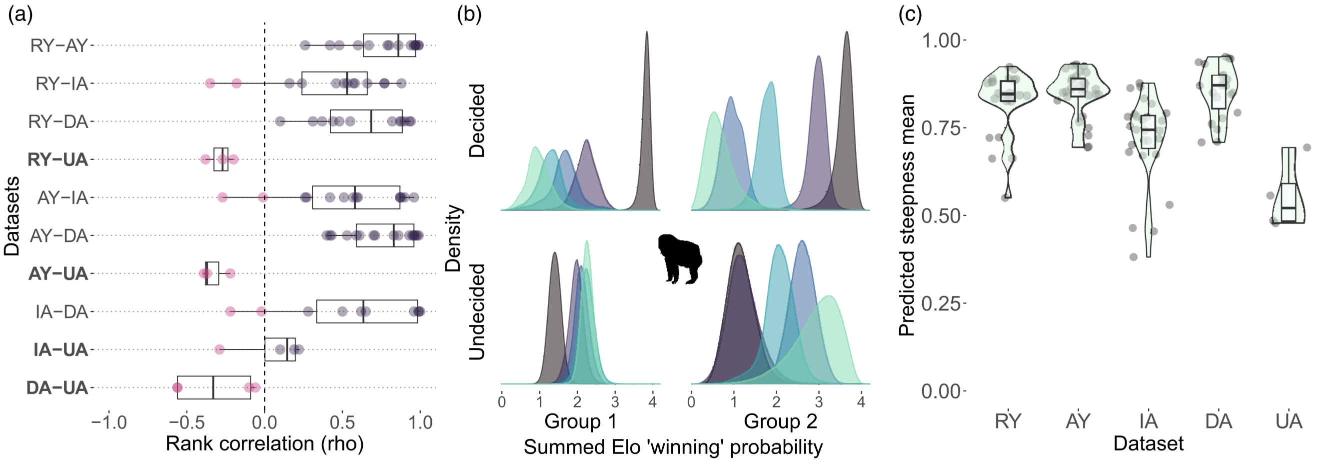


FIGURE 2 Differences of ranks and hierarchies inferred from different behavioural data sets. (a) The correlation coefficient among ranks inferred from different data sets. Each data point correspond to a matrix pair, negative correlation is depicted in red and undecided aggression is depicted in bold. (b) An extreme example of reversed individual ranks of male mandrills (data from (Setchell & Dixson, 2001)) when inferred from decided (top) and undecided (bottom) aggression. Panels on the left correspond to group 1 and panels on the right to group 2. Each individual is represented by a posterior distribution and a colour. (c) Predicted mean steepness in social hierarchies inferred from different data sets. The fitted values of the GLMM are shown on the *y*-axis. RY, ritualized yielding; AY, all yielding; DA, decided aggression; IA, initiated aggression; UA, undecided aggression.

3.1.3 | Initiated aggression versus other data sets

When I compared individual ranks inferred from initiated aggression, with ranks inferred from the other four data sets, the results were more inconsistent (Figure 2a: rows including IA) likely due to the negative correlation between ranks inferred from decided and undecided aggression (whose combination constitutes initiated aggression; Figure 1). Specifically, ranks inferred from initiated aggression showed a correlation coefficient of 0.37 ± 0.35 (±S.D.; confidence: 76%) with those inferred from ritualized yielding, 0.58 ± 0.36 (confidence: 88%) with those inferred from all yielding, 0.57 ± 0.41 (confidence: 85%) with those inferred from decided aggression and 0.06 ± 0.15 (confidence: 58%) with those inferred from undecided aggression (Figure 2a and Table 2: rows/columns RY-IA, AY-IA, IA-DA and IA-UA). The number of dyadic interactions of initiated aggression was positively correlated with the number of interactions of ritualized yielding (mean rho ± S.D.: 0.46 ± 0.14; confidence: 98%), all yielding (0.65 ± 0.26; 98%), decided aggression (0.68 ± 0.28; 99%) and undecided aggression (0.59 ± 0.33; 95%; Table 2: columns RY-IA, AY-IA, IA-DA and IA-UA, values in parentheses).

The correlation of ranks inferred from different data sets was greater when more individuals were included in the hierarchy and when the maximum steepness was greater (likely because in more despotic systems, different behaviours infer similar hierarchies; Table S4; Supporting Information: 'Despotism, number of individuals and rank correlation').

3.2 | Steepness

The steepness mean ranged from 0.11 to 0.97 with a mean (±S.D.) of 0.79 ± 0.19. The mean steepness values of hierarchies inferred from ritualized yielding, all yielding or decided aggression (i.e. all the three data sets including exclusively decided interactions) were little different among them (95% CIs crossed zero) but greater than those of hierarchies inferred from initiated or undecided aggression (Table 3a; Figure 2c). These results were qualitatively similar to the results of the phylogenetically controlled model (Table 3b; see also Figure S1). Accordingly, when I added to the model the sex composition of the matrix (female only, male only or intersexual), the effect of the behavioural data set remained qualitatively similar and the mean steepness values showed little differences among groups of different sex composition (95% CIs crossed zero; Table S5).

The steepness uncertainty was on average 0.10 ± 0.07, ranging from 0.01 to 0.36, and it was greater when the mean number of interactions per individual and the number of individuals were lower (Table 3c). The steepness uncertainty values of hierarchies inferred from ritualized yielding (Table 3c), all yielding or decided aggression were little different among them but lower than those of hierarchies inferred from initiated or undecided aggression (Figure S2a), although the 95% CI of undecided aggression crossed zero (Table 3c).

4 | DISCUSSION

The ranks and hierarchies inferred from data sets including undecided interactions differed markedly from those inferred from data sets including exclusively decided interactions. First, individual ranks inferred from undecided aggression were negatively correlated with those inferred from decided interactions (Figure 2a,b). Second, the number of dyadic undecided aggressive interactions was not correlated with the number of any kind of decided interactions. Third, the steepness values of hierarchies inferred from data sets including undecided interactions were generally lower than steepness values inferred from data sets including exclusively decided interactions (Figure 2c). The combination of these results likely elucidates why the uncertainty of steepness values inferred from initiated aggression (i.e. decided and undecided aggression combined) was greater than that inferred from exclusively decided or exclusively undecided interactions. Altogether, these results call into question the validity of the use of undecided aggression in lieu of or in combination with decided agonistic interactions in order to infer social hierarchies. In fact, they may suggest that, in contrast to decided aggression, undecided aggression can reflect low social status of aggressors because, for example, powerful individuals ignore aggression initiated by less powerful individuals (Rowell, 1974).

Hierarchies inferred from data sets including exclusively decided interactions were generally similar. Yet, the different kinds of these interactions can show important functional differences. Given that a major function of hierarchical relationships is to resolve contests economically (Bernstein, 1981; Rowell, 1974), the need of an individual to elicit yielding of another through aggressive means might, in fact, reflect a weak hierarchical relationship (Lewis, 2022). Conversely, ritualized yielding might serve to reassure powerful individuals of their position with no need of aggression (de Waal, 1989) and might be a better indicator of rank (Rowell, 1974) as the actions of subordinate individuals are likely more influential in the stability of a relationship (Jensen & Wood-Gush, 1984; Kaufmann, 1983). Indeed, greater aggression rates are often associated with unstable social hierarchies (Jensen & Wood-Gush, 1984; Sapolsky, 1993). More generally, recent literature adopts the concept of 'power' to describe dyadic competitive asymmetries that allow one individual to make another do something; calling for behavioural measures that, in contrast to aggression, do not necessarily reflect force or threat of force (Lewis, 2002, 2022). Ritualized yielding interactions might constitute such a measure since they can reflect more comprehensive power relationships emerging from prestige (i.e. based on valued knowledge and skills), leverage (i.e. based on resources that cannot be taken by force, such as female eggs) or dominance (i.e. based on coercion/ intimidation; Lewis, 2002; Maner, 2017).

At first glance, the generally comparable hierarchies inferred from decided aggression or ritualized yielding seem to suggest that these behaviours can be safely pooled, as commonly observed (Hauver et al., 2013; Richter et al., 2009; Surbeck & Hohmann, 2013). Although such pooling might be crucial in enriching data sets used to infer social hierarchies, especially in situations

TABLE 3 Results of the GLMMs testing the influence of different behavioural data sets on (a) mean steepness, (b) mean steepness (phylogenetically controlled model including only mammals) and (c) steepness uncertainty of the inferred hierarchies.

Response variable		(a) Steepness			(b) Steepness (phylo)			(c) Uncertainty		
Fixed/random f.	**Level**	**Estimate**	**Error**	**CI 95%**	**Estimate**	**Error**	**CI 95%**	**Estimate**	**Error**	**CI 95%**
Intercept		1.32	0.31	[0.74, 1.98]	1.3	0.4	[0.52, 2.12]	−1.38	0.18	[−1.72, −1.04]
Data set	AY	0.16	0.19	[−0.22, 0.54]	0.26	0.21	[−0.15, 0.65]	0.03	0.11	[−0.19, 0.26]
(Ref: RY)	IA	−0.83	0.19	[−1.19, −0.46]	−0.88	0.2	[−1.26, −0.5]	0.44	0.11	[0.23, 0.65]
	DA	0.22	0.21	[−0.2, 0.63]	0.12	0.22	[−0.31,0.55]	0.07	0.12	[−0.16, 0.3]
	UA	−0.74	0.32	[−1.35, −0.12]	−0.78	0.31	[−1.39, −0.16]	0.29	0.17	[−0.04, 0.61]
Nr. of individuals		0.05	0.02	[0, 0.09]	0.05	0.02	[0, 0.09]	−0.07	0.01	[−0.1, −0.05]
Mean interactions		0	0	[−0.01, 0]	0	0	[−0.01, 0]	−0.01	0	[−0.02, −0.01]
Study		0.52	0.16	[0.22, 0.83]	0.54	0.16	[0.26, 0.89]	0.24	0.09	[0.06, 0.42]
Species		0.33	0.17	[0.04, 0.69]	0.31	0.18	[0.02, 0.71]	0.17	0.08	[0.02, 0.35]
Phylogeny		—	—	—	0.33	0.27	[0.01, 1]	—	—	—

Note: The estimates, errors and 95% credible intervals are shown. A horizontal line separates fixed and random factors.

Abbreviations: AY, all yielding; DA, decided aggression; IA, initiated aggression; mean interactions, mean number of interactions per individual; number of individuals, number of individuals in the hierarchy; RY, ritualized yielding (reference category); UA, undecided aggression.

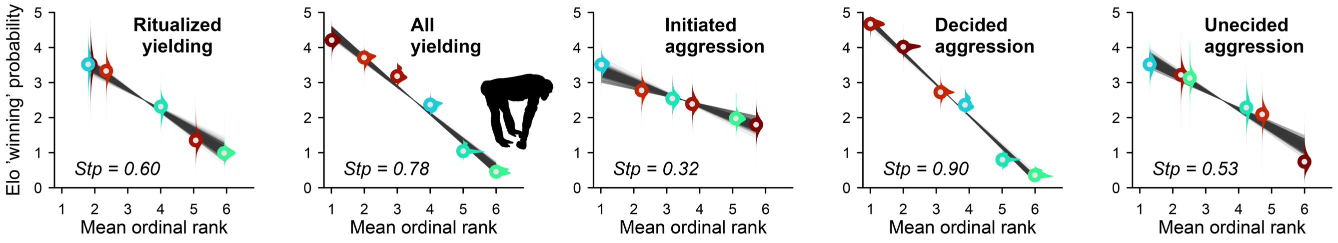


FIGURE 3 Order of individuals and steepness of the hierarchies inferred from the five different behavioural data sets of a bonobo group (Vervaecke et al., 2000). The steepness (Stp) is represented by the slope of the regression line between the summed 'winning' probability and the mean ordinal rank. Each individual is represented by a posterior distribution and a colour. Shades of red represent females and shades of blue/green males. While the steepness values are similar (e.g. between ritualized yielding and undecided aggression), the order of the individuals can be strikingly different. Similarly, the average proportion of males outranked by females can differ highly: All females rank higher than all males in the hierarchies inferred from all yielding and decided aggression but in the hierarchy inferred from undecided aggression males generally rank higher than females (see also Figure S2b).

where agonistic interactions are rare or observations difficult (e.g. in marine organisms), it might not always be biologically justified. First, the rarity or absence of agonistic interactions can be as informative as the presence of it, for example, reflecting egalitarian relationships. Second, my results show that the correlation coefficient of ranks inferred from the two data sets can vary greatly (from 0.1 to 0.94; Figure 2a: row RY-DA), potentially suggesting significant interspecies variability in directional consistency of different behaviours: The direction of yielding might be more consistent than that of aggression in baboons (Rowell, 1966) but not in bonobos (Vervaecke et al., 2000). Additionally, this variation might partially reflect categorization inconsistencies since supplants (Table 1b,c) are occasionally categorized as decided aggression instead of ritualized yielding (Bromley, 1991; Kappeler et al., 2022). Previously developed frameworks that can evaluate if certain behaviours convey similar information, and thus, they can be pooled, may facilitate relevant decisions in hierarchy inference (van der Marel et al., 2021).

The combination of the aforementioned variability in the correlation of ranks inferred from decided aggression and ritualized yielding with the similarity of steepness values of hierarchies inferred from these two data sets suggests that a similarity between group (hierarchy) properties might not always entail similarity between individual (rank) properties and vice versa. Figure 3 illustrates a relevant example where similar steepness values emerge from strikingly different individual hierarchical orders of bonobos. Notably, in this group (Vervaecke et al., 2000), decided aggression infers greater female power over males than ritualized yielding does (see also 'Sex biases' in Supporting Information). This inconsistency suggests that, before merging different behavioural data sets, researchers should test if, in their study system, the hierarchies inferred from each data set separately produce similar results at both group and individual levels. If this is not the case, they may choose the data set/hierarchy that predicts more accurately the trait they are interested in, such as priority of access to a resource. That is, they should choose behavioural data sets based on a functional social compound and not based on the properties of the hierarchy itself that would likely represent circular reasoning. From a methodological perspective, and for a given data set, it might be reasonable to aim, for example, at a social hierarchy that is most consistent with a linear order (de Vries, 1998), but choosing the data set that produces the most linear or steep hierarchy might constitute a logical fallacy: '*asymmetry, transitivity, linearity, and the like are not rules that animals must obey but regularities for the scientist to discern*' (Altmann, 1981).

The differences in ranks inferred from ritualized yielding and other data sets might also result from the fact that the patterns of agonistic interactions (Bernstein, 1981) and the interpretation of ritualized behaviours (Flack & de Waal, 2007) differ within and outside established relationships. Ritualized yielding might be more common among familiar group mates and those with large rank differences, while aggression might be more common among unfamiliar individuals and those with low rank differences (but see also Chaine et al., 2018). The collected data set was taxonomically biased towards Cercopithecine primates where females are usually philopatric and males disperse from their natal groups (Furuichi et al., 2015), meaning that female–female relationships are often better established than female–male or male–male relationships. This bias might have indeed influenced my results: The confidence of a positive rank correlation was 100% among all matrix pairs for adult female crested macaques (*Macaca nigra*), but varied greatly for adult male mandrills (*Mandrillus sphinx*; Table 2). Nonetheless, I observed substantial variation even within sex classes of Cercopithecines: The ranks inferred from ritualized yielding and initiated aggression in female-only hierarchies were positively correlated in Hanuman langurs (*Semnopithecus entellus*) but negatively correlated in guerezas (*Colobus guereza*; Figure 2a and Table S2: RY-IA). Altogether, the observed variation in correlation patterns among ranks and steepness of hierarchies inferred from different behavioural data sets might partially reflect taxonomic proximity, social organization or intersexual relationships (see Figure 3 and Figure S2b). Yet, my results on steepness were qualitatively similar when I controlled for phylogeny (Table 3b) or sex composition (Table S5).

Future work on an extended data set may strengthen or alleviate the claims of this study. However, I present here strong evidence that at least in some mammals, different data sets can infer different hierarchies, and thus, the nature of interactions should be considered when assessing the comparability of any methods. I suggest that the use of ritualized yielding and certainly the use of decided over undecided interactions to infer social hierarchies should be preferred. Decided interactions are observed in insects (Ortius & Heinze, 1995), birds (Dawson & Mannan, 1991), ungulates (Vervaecke et al., 2007), humans (Strayer & Trudel, 1984), other primates (Smit et al., 2022), fish (Nakano, 1994), rodents (Farentinos, 1972), carnivores (Hauver et al., 2013), pinnipeds (Schusterman & Dawson, 1968) and other taxa, suggesting that a relatively consistent relationship between specific behaviours and hierarchical relationships across behavioural studies might be feasible.

AUTHOR CONTRIBUTIONS

Nikolaos Smit conceived and designed the study, collected data from the literature, performed statistical analyses and wrote the manuscript.

ACKNOWLEDGEMENTS

I would like to thank Elise Huchard and Dieter Lukas for their comments on a previous version of the manuscript. For Figure 1, I used and edited silhouette icons of baboons created by Ben Kawam who also provided comments in an early draft of the manuscript. Finally, I would also like to thank the people who collected the data used for this study, the authors who made these data accessible as well as the editorial team and reviewers for their constructive feedback. In Table 2 and graphical abstract, I used silhouette icons from http://phylopic.org. Publication costs were covered by the Max Planck Society.

CONFLICT OF INTEREST STATEMENT

I declare I have no competing interests.

DATA AVAILABILITY STATEMENT

Data available from the Zenodo repository https://doi.org/10.5281/zenodo.13883781 (Smit, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. The collected data from the literature.

Table S2. Correlations among dyadic frequencies of interactions and ranks inferred from different data sets.

Table S3. Results of GLMM testing the influence of different behavioural data sets on mean steepness based on David scores.

Table S4. The probability of correlation between the ranks inferred from two different behavioural data sets as a function of the maximum steepness calculated for the species and the number of individuals in the hierarchy.

How to cite this article: Smit, N. (2024). Hierarchies inferred from different agonistic behaviours are not always comparable. *Journal of Animal Ecology*, *93*, 1947–1959. https://doi.org/10.1111/1365-2656.14203