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Quantifying within-group variation in sociality—covariation among metrics and patterns across primate groups and species

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Abstract

It has long been recognized that the patterning of social interactions within a group can give rise to a social structure that holds very different places for different individuals. Such within-group variation in sociality correlates with fitness proxies in fish, birds, and mammals. Broader integration of this research has been hampered by the lack of agreement on how to integrate information from a plethora of dyadic interactions into individual-level metrics. As a step towards standardization, we collected comparative data on affinitive and affiliative interactions from multiple groups each of five species of primates to assess whether the same aspects of sociality are measured by different metrics and indices. We calculated 16 different sociality metrics used in previous research and thought to represent three different sociality concepts. We assessed covariation of metrics within groups and then summarized covariation patterns across all 15 study groups, which varied in size from 5 to 41 adults. With some methodological and conceptual caveats, we found that the number of weak ties individuals formed within their groups represented a dimension of sociality that was largely independent from the overall number of ties as well as from the number and strength of the strong ties they formed. Metrics quantifying indirect connectedness exhibited strong covariation with strong tie metrics and thus failed to capture a third aspect of sociality. Future research linking affiliation and affinity to fitness or other individual level outcomes should quantify inter-individual variation in three aspects: the overall number of ties, the number of weak ties, and the number or strength of strong ties individuals form, after taking into account effects of social network density.

Significance statement

In recent years, long-term studies of individually known animals have revealed strong correlations between individual social bonds and social integration, on the one hand, and reproductive success and survival on the other hand, suggesting strong natural selection on affiliative and affinitive behavior within groups. It proved difficult to generalize from these studies because they all measured sociality in slightly different ways. Analyzing covariation between 16 previously used metrics identified only three rather independent dimensions of variation. Thus, different studies have tapped into the same biological phenomenon. How individuals are weakly connected within their group needs further attention.

Introduction

Among group-living animals, there is pronounced variation among species, populations, and groups in social structure that is the content, quality, and patterning of social relationships that emerge from repeated social interactions among the same partners (Hinde 1976). These social interactions involve affinitive (spatial), affiliative (friendly), and agonistic

(aggressive and submissive) behaviors; patterns of sexual behavior and care-taking concern other aspects of the social system (Kappeler 2019). The sociality of an individual is its position within the social structure, which can be described in terms of its spatial positioning in the group, its affiliative relationships, its social status/dominance rank, or a combination thereof.

Within-group variation in sociality should have profound effects on fitness (Silk 2007). Group-living is thought to evolve when the costs to the individual are exceeded by the benefits of permanent association relative to alternatives outside the group (Krause and Ruxton 2002). Group-living can be costly in terms of increased feeding competition, conspicuousness to predators, infection risk, mating competition, or consensus costs from collective decision-making (Freeland 1976; Ward and Webster 2016). Group-living may confer benefits in terms of reduced predation risk resulting from dilution effects, cooperative defense or enhanced vigilance, as well as in terms of cooperative defense of food or shelter, enhanced foraging efficiency, thermoregulation, and social information (Alexander 1974; Clutton-Brock 1974; Wrangham 1979). Yet, neither costs nor benefits of group-living are likely to be the same for all group members, because costs and benefits vary with relative spatial position in the group (Bumann et al. 1997; Voelkl et al. 2015; Sperber et al. 2019), with dominance rank (Majolo et al. 2012; Snyder-Mackler et al. 2020), or with the frequency and diversity of friendly physical contacts with other group members (Balasubramaniam et al. 2019; Müller-Klein et al. 2019). This means that different positions in a given social structure are associated with different costs and benefits.

There is a long history in behavioral ecology to study the fitness effects of variation in dominance rank (Sade et al. 1976; Smith 1981), whereas the adaptive benefit of the affiliative and affinitive facets of sociality have gained attention only more recently. Dominance relationships are often transitive so that individuals can be ordered along a linear hierarchy (de Vries 1998) that is generally rather robust across different methods of hierarchy construction (Neumann et al. 2011; Sánchez-Tójar et al. 2017). How best to relate dominance to outcome variables depending on the research question and the competitive regime of the species is discussed elsewhere (Levy et al. 2020) and will be ignored from here on. We only consider quantification of affinity and affiliation (see glossary), which are often discussed together in the literature, because being spatially close to each other is a prerequisite for friendly interaction. There is to date no broad agreement on how to quantify sociality, partly due to the fact that affinitive and affiliative relationships are less transitive. Nevertheless, evidence is accumulating that links affinitive and affiliative sociality to reproduction and longevity, highlighting its evolutionary importance.

A recent review on the sociality-fitness link summarized 21 publications from 16 studies on 14 species of cetaceans, primates, rodents, and ungulates that used 16 different individual-level affinity and affiliation metrics, highlighting the lack of consensus in the metrics applied (Ostner and Schülke 2018): the metrics were degree, strength, and their variance, count and strength of only the strong ties, number of close kin as a proxy for the count of strong ties, count of only the weak ties, as well as Eigenvector and betweenness centrality; these metrics were taken from networks with ties representing composite sociality indices, close proximity, collaboration in coalitions, different association indices, rate of aggression, or partner preferences. To date, only a few studies have assessed the covariation among these different affinity and affiliation metrics and the relative strength of their correlation with the same fitness components (Cheney et al. 2016; Ellis et al. 2019; Bray et al. 2021).

The lack of consensus in how to quantify sociality has hampered comparative analyses and assessment of the generality of findings. It remains largely unknown whether different studies have detected the same or several different biological phenomena when they report sociality-fitness correlations (Ostner and Schülke 2018; Silk et al. 2018; Snyder-Mackler et al. 2020). Different mechanisms linking variation in sociality could theoretically be fueled by different aspects of sociality (Ostner and Schülke 2018). For example, if fitness effects result from increased access to information, occupying a central/brokering position that connects otherwise unconnected parts of the social structure should be most beneficial (Brent 2015; Sueur et al. 2011a), whereas in societies where fitness effects are driven by coalitionary support in competition for social status, individuals with a few very strong social bonds might have the most beneficial position (Ostner and Schülke 2018; Sosa et al. 2021)

The value of assessing covariation between different sociality metrics extends beyond their application to the questions mentioned above. Other research areas that require measuring individuals' position in affinitive and affiliative social structure include social cognition (Almeling et al. 2016; Platt et al. 2016), comparative psychology (Massen and Koski 2014), social neuroscience (Cacioppo and Cacioppo 2012), and social psychopathology (Bauman and Schumann 2018).

A first critical decision facing efforts to study variation in sociality are the types of behavioral data to use when constructing sociality metrics. It is currently debated, exemplified here for studies linking sociality and fitness, whether sociality is best indexed from affinitive behavior alone (Ellis et al. 2017), only from direct affiliative interactions involving body contact like grooming (McFarland et al. 2015), in parallel but separately from both types of data (Bray and Gilby 2020; Brent et al. 2013), from a combination that integrates correlated affinitive and affiliative behaviors (Silk et al.

2006a, 2010a), or from a combination that also includes agonistic behavior (Crockford et al. 2013). In the following, we will refer to these choices and corresponding behavioral measures as different sociality indices (Box 1). The choice of index may depend on the research question, average frequencies of behaviors, observational data collection methods, and visibility of group members as they affect the accuracy of the behavioral measure (Sosa et al. 2021).

BOX 1: Glossary

Sociality is an individual's position in the social structure (our definition).

Social structure is the content, quality, and patterning of social relationships emerging from repeated social interaction among the same individuals (Hinde et al. 1976)

Social status/dominance is an individual's position in the dominance hierarchy of a group, a well-studied aspect of sociality that is excluded from analyses here.

Sociality indices here are behavioral measures either of affinity or affiliation or an integration of several affinity and/or affiliation measures into composite indices.

Affinitive behavior establishes, maintains, and terminates spatial proximity between partners.

Affiliative behavior is any form of friendly, peaceful social behavior.

Concepts are abstract ideas about dyadic social relationships and how they scale up from the dyad to the individual to the group with consequences for individual social position in the group

Sociality metrics as used here are different ways of aggregating dyadic information at the individual level for the quantification of sociality depending on the concept under investigation.

A second issue is that inter-individual variation in sociality has been examined with at least three different concepts in mind: social bonding, social integration, and indirect connectedness, which may or may not represent three independent dimensions of within-group variation in sociality. The concept of social bonding relates to attachment theory in psychology and the formation of friendships in humans (Silk 2002; Dunbar and Shultz 2010; Massen et al. 2019) and concerns the strongest affiliative relationships individuals form. Social integration is the broader embeddedness of the individual in its social group by interactions or association with different partners. Weak connections have been suggested to serve an independent adaptive function of social integration and therefore to deserve special scrutiny (vanderWaal et al. 2016; McFarland et al. 2017). The third concept considered here is indirect connectedness (structural connectedness in Ellis et al. (2019)), i.e., inter-individual variation in social embeddedness resulting from variation in how also an individual's direct partners are connected to other group members (in a "friend-of-a-friend" manner, Brent 2015) and how an individual is positioned relative to all other nodes in the network, i.e., in the social structure resulting from affinitive and affiliative behavior of all group members. Different aspects of indirect connectedness can be construed that relate to different biological phenomena (Sosa et al. 2021), e.g., the friends of friends may provide an extended network of cooperators, whereas a broader perspective is needed to assess individual roles in network diffusion of information or parasites. The link between social bonding, social integration, and indirect connectedness remains poorly resolved and may vary to some extent among species and social groups.

As a step towards unifying research on this key topic in behavioral ecology, we collected social behavior data from 15 social groups from 5 primate species representing the three independent transitions to group living in the primate order (Kappeler and Pozzi 2019): two species of gregarious lemurs (*Eulemur rufifrons* and *Propithecus verreauxi*), two species of macaques (*Macaca assamensis* and *M. sylvanus*), and Western chimpanzees (*Pan troglodytes verus*). These data were subjected to the same procedures (see text Box 2). We used three sociality indices, all measured at the dyadic level: the time spent in close proximity, time spent grooming, and a dyadic composite sociality index. For each of the indices, we integrated these dyadic data at the individual level into 16 sociality metrics (Box 1, Table 1): strength, degree, counts and strength of strong or weak ties with different thresholds,

betweenness, and Eigenvector centrality (Table 2). These metrics have been used in previous research on the sociality-fitness link and can be grouped into the three concepts of social bonding, social integration, and indirect connectedness. The specific aim of this study was to obtain quantitative measures of sociality to assess their similarity, with the ultimate goal of providing future studies of social behavior with recommendations to facilitate comparative studies.

We report per sociality index, within-group, across-individual correlations of the 16 metrics, and how the correlation between pairs of metrics varies across our study groups and

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BOX 2: Analytical strategy

1) <u>Record</u> frequency and duration of different social <u>behaviors</u> (grooming, contact sitting, close proximity)

2) <u>Build</u> separate weighted <u>social networks</u> for each of three <u>sociality indices</u> (time spent in close proximity, grooming duration, Dyadic Composite Sociality Index DSI)

3) <u>Integrate information at the individual level</u> with 16 different <u>metrics</u> (see main text) representing 3 <u>concepts</u> (social bonding, social integration, indirect connectedness)

4) Build pair-wise <u>correlation matrices of all metrics across individuals</u> in a group

5) <u>Summarize</u> correlation matrices across groups (mean and standard deviation) <u>across 15 social groups</u>

6) <u>Run non-metric cluster analysis on summary matrix</u> (and plot both together) to identify similarities between metrics in covariation patterns (Fig. 1)

7) Assess <u>congruence</u> between <u>clusters and</u> *a priori* <u>concepts</u>

8) Assess strength and direction of <u>covariation within and between clusters</u>

9) Describe variation in covariation <u>patterns across groups</u>

10) Compare results <u>between indices</u>

11) <u>Consider methodological limitations</u> about network density as a function of group size and sampling effort

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species to investigate whether the same aspect of sociality is measured by different metrics, concept, or indices. In order to achieve this, we (1) assess the generality of covariation patterns and whether metrics within one concept measure the same. (2) We quantify the covariation between metrics of different concepts of sociality (social bonding, social integration, indirect connectedness) and assess whether metrics from different concepts form separate clusters explaining different aspects of sociality. The number of weak ties for example (relative to some threshold) might capture an aspect of sociality that is different from (and therefore uncorrelated to) other metrics of direct or indirect connectedness or social bonding (McFarland et al. 2017).

Furthermore, we address a number of debates in the current literature on the evolution of affiliative behavior and investigate if affiliation and affinity tend to measure the same aspect of sociality. To this end, we (3) compare results for networks built from three sociality indices to assess how covariation patterns between metrics differ between these networks. Finally, we (4) revisit a possible trade-off between the quantity and the quality of affiliative relationships (Archie et al. 2014; Ellis et al. 2019) that would help explain the maintenance of inter-individual variation in relationship quality in a population. Beyond these conceptual issues, we address a number of technical matters concerning the construction of composite sociality indices, thresholds

Table 1 Concepts about individual level within-group variation in sociality (affinity and affiliation), their justification, and the metrics that have been employed to quantify them (see text for further references)

Concept	Justification	Metrics	Examples
Social bonding	Social bonds are strong, equitable, lasting affiliative relationships; without clear classification, strength can be used to quantify bonding	Number of strong ties (> average) Strength of strong ties (> average) Strength of strong ties (sign. > average) Strength of top 3 ties	McFarland et al. (2017) Silk et al. (2018) Kalbitzer et al. (2017) Thompson and Cords (2018)
Social integration/direct connectedness	Individuals differ in whether, how often, and how long they interact with every other group member	Number of all ties (degree) Strength of all ties (strength) Number of weak ties (< average)	McFarland and Majolo (2013) Silk et al. (2013) McFarland et al. (2017)
Social integration/indirect connectedness	Individuals differ in how they are indirectly connected to all other group members and in how their direct partners differ in direct connectedness	Eigenvector centrality Betweenness	Brent et al. (2013) Cheney et al. (2016)

differentiating weak from strong ties, sampling intensity, group size effects, and overall network density.

Methods

Data collection

Data for these analyses were collected with support from the German Research Foundation for the Research Group "Sociality and Health in Primates" (DFG FOR 2136). All data were collected over a period of maximum of 1 year during focal animal protocols continuously recording the frequency and duration of allo-grooming and (except for chimpanzees) contact sitting, and approaches into and departures from close proximity of the focal animal, using a 1m sphere for the smaller lemurs and 1.5m for the larger macaques. For chimpanzees, which exhibit high fission-fusion dynamics (Aureli et al. 2008), we recorded membership in the same subgroup at 30-min intervals and used these data to calculate a dyadic association index (Nishida 1968). It was not possible to blindly record data, because our study involved focal animal sampling in the field.

Wild Assamese macaques (*M. assamensis)* from four study groups were observed from dawn till dusk for 4–14 days every month from January through December 2015 (except SO in December, SS in February and September) in their natural habitat at Phu Khieo Widllife Sanctuary, which is part of a >6,500km^2 system of protected natural areas in Northeastern Thailand (Ebenau et al. 2019; De Moor et al. 2020). Data on Barbary macaques (*M. sylvanus*)

Table 2 List of metrics used to characterize inter-individual variation in three different dimensions of sociality

Nr.	Concept	Metric
1	Social bonding	Count of strong ties (strength > 0.9 percentile)
2		Count of strong ties (strength > 3rd quartile)
3		Count of strong ties (strength > mean)
4		Strength of strong ties (top 3* ties of individual)
5		Strength of strong ties (strength > 0.9 percentile)
6		Strength of strong ties (strength > 3rd quartile)
7		Strength of strong ties (strength > mean)
8	Social integration	Strength (sum of all ties)
9		Degree (count of all ties)
10		Count of weak ties (strength < mean)
11		Count of weak ties (strength < 1st quartile)
12		Count of weak ties (strength < 2nd quartile)
13		Count of weak ties (strength < 3rd quartile)
14		Count of weak ties (strength < 0.9 percentile)
15	Indirect connectedness	Eigenvector centrality (weighted)
16		Betweenness (weighted)

*See text for details on number of top ties

were collected from 7 am through 18 pm on most days every month from June through December 2014 in group C and June through November 2015 in group H in a 20-ha forested outdoor enclosure from two out of three freely mingling groups at Affenberg Salem, Germany (Müller-Klein et al. 2018). Data on both lemur species came from Kirindy Forest, a tropical dry forest in central western Madagascar (Sperber et al. 2019; Rudolph et al. 2020). Verreaux's sifakas, *P. verreauxi*, were observed every month from January through December 2017 (except group E in November and J in December) with data collection starting at 7 am and terminated at 4 pm. Red-fronted lemurs, *E. rufifrons*, were observed for several days every month from January through December 2015 in group A and May 2015 through April 2016 in groups F and J from 7 am to 4 pm. Three neighboring groups of chimpanzees (*P. troglodytes verus*) were observed in Taï National Park, Ivory Coast (Wittig and Boesch 2019), on average for 12.4 days per month per group between January and December 2018 during nest to nest follows (sunrise to sunset). The composition of all study groups is reported in Table 3 together with the observation effort. Only for lemurs, we included juveniles between weaning and onset of sexual maturity, because otherwise networks would have been too small for our analyses. In total, our analyses included 17,998 hours of focal animal data.

Sociality indices

We provide an overview of our analytical concept in Box 2. For each group, we built three social networks based on (a) the duration of grooming in a dyad, (b) the time a dyad spent in proximity, or (c) a dyadic composite sociality index (DSI) built from affiliative and affinitive behaviors (Silk et al. 2013) all controlled for dyadic observation time. The DSI is a data reduction procedure that can be constructed from any number and kind of social behavior measures (e.g., grooming duration, frequency of embraces, kisses, or play initiations, frequency of aggression), if they are strongly associated. In this sense, the DSI serves a similar purpose as a principle component analysis.

The DSI relates sociality of the dyad to the mean across all dyads in the group and thus has a minimum of zero if the dyad partners never associated and never interacted, a mean of one, and an open upper end. For a behavioral measure to be included in the index, we required the mean raw count of the behavior per dyad to be >2 to avoid that a single observation puts the dyad above the average. This rule may be replaced by more advanced assessments of reliability and may need to be reconsidered in any future studies of highly clustered groups where well-separated

subgroups never interact and bring down the mean interaction frequency.

For the DSI to work as a data reduction procedure, all behavioral measures *i* have to be significantly positively correlated across dyads, which we tested using pair-wise Kendall row-wise matrix correlations with 10,000 randomizations of columns run on symmetric matrices of dyadic values in MatMan 1.1. (de Vries et al. 1993). Since this condition was not fulfilled for all behavioral measures in all groups, DSI was constructed from a different set and number of behavioral measures for different groups of the same or different species, but always from positively correlated behaviors. For each behavioral measure, the raw duration or frequency within a dyad *xy* was divided by the sum of the focal animal observation time for both partners (to account for inter-individual variation in observation effort), the resulting dyadic values f_{xy} were divided by their mean across all dyads of the group $\bar{f}_i$, then summed across all components, and finally divided by the number of components *d* (Silk et al. 2013). Thus, variation in each standardized component is given the same weight, and a single act of a rare or short behavior (like grooming) has a larger effect on the DSI than a single act of a frequent or long-lasting behavior (like sitting in close proximity without body contact). This approach serves to avoid situations in which variation in frequent behaviors masks variation in rarer behaviors, but it also assigns a single event of a frequent behavior less weight on the index.

$$DSI_{xy} = \frac{\sum_{i=1}^{d} \frac{f_{ixy}}{\bar{f}_i}}{d}$$

Following the procedures outlined above, the DSI was built from six components (the duration and count each of grooming, contact sitting, and close proximity) for all groups of both macaque species, sifaka groups E and J, as well as RedFrJ (Supplementary Material S1). Since data on time spent in close proximity were either not available or did not correlate with the other components, the DSI was built from 4 components (duration and count each of grooming and contact sitting) for the remaining three lemur groups RedFrA, RedFrF, and SifakaF. For chimpanzee group S, the DSI had three components (the duration and count of grooming and the dyadic association index). For the remaining two chimpanzee groups E and N, the DSI summarized variation in duration and count of grooming only, because neither grooming count nor duration covaried with the association index and a priori grooming was deemed the better indicator of dyadic affiliative relationship strength (see below for a discussion of affinity versus affiliation). We emphasize again that duration and count for the entire study period were corrected for the sum of observation hours on both partners of a dyad and therefore

Table 3 Study groups with species, adult group size, number of possible dyads, and observation effort in hours per group, average individual, and average dyad. We defined as juvenile lemurs here all non-reproductive individuals older than 1 year

Species	Group	Group size	Dyads	Observation time (per group/indiv./ dyad)
Assamese macaques (*Macaca assamensis*)	AssMcMS	29 adults (18F, 11M)	406	3235.4 / 111.6 / 8.0
	AssMcSS	16 adults (11F, 5M)	120	1097.4 / 68.6 / 9.1
	AssMcMO	28 adults (15F, 13M)	378	2855.1 / 100.8 / 7.5
	AssMcSO	16 adults (9F, 7M)	120	1296.8 / 81.0 / 10.8
Barbary macaques (*Macaca sylvanus*)	BarbMcC	36 adults (20F, 16M)	630	1594.8 / 44.3 / 2.5
	BarbMcH	41 adults (23F, 18M)	820	1815.3 / 44.3 / 2.2
Western chimpanzees (*Pan troglodytes verus*)	ChimpE	14 adults (9F, 5M)	91	1803.2/128.8/19.8
	ChimpN	12 adults (8F, 4M)	66	1562.5 / 130.2 / 23.6
	ChimpS	20 adults (14F, 6M)	190	1504.3 / 75.2 / 7.9
Red-fronted lemurs (*Eulemur rufifrons*)	RedFrA	9 incl. 1 juvenile (4F, 5M)	36	311.5 / 34.6 / 8.7
	RedFrF	5 incl. 1 juvenile (2F, 3M)	10	133.3 / 26.7 / 13.3
	RedFrJ	10 incl. 2 juveniles (5F, 5M)	45	212.6 / 23.6 / 5.9
Verreaux's sifakas (*Propithecus verreauxi*)	SifakaE	6 incl. 2 juveniles (2F, 4M)	15	162.4 / 27.1 / 10.8
	SifakaF	9 incl. 5 juveniles (4F, 5M)	36	243.1 / 27.0 / 6.7
	SifakaJ	7 incl. 3 juveniles (3F, 4M)	21	170.4 / 24.3 / 2.0

represent a duration per observation hour and frequency per observation hour.

Sociality metrics by concept

As the next step, we built undirected, weighted social networks with ties between individuals representing either the DSI, the corrected dyadic grooming time, or corrected dyadic time spent in proximity. For each network, we calculated 16 different sociality metrics that integrated information at the individual level; in the following, we provide descriptions of these metrics for the DSI network. To measure social bonding (Silk 2002; Ostner and Schülke 2014), we counted the number and measured the strength of strong ties. Since it is not possible to define the threshold for a strong tie from observational data alone, we followed Ellis et al. (2019), who used several thresholds, and counted the number of strong ties with strength above (1) the 0.9 percentile, (2) the 3rd quartile, and (3) the mean value, and we measured strength of the strongest ties using (4) the top three connections per individual (Schülke et al. 2010; Silk et al. 2010b; McFarland et al. 2017; Campos et al. 2020) and at the group level (5) the 0.9 percentile, (6) the 3rd quartile, and (7) the mean tie strength. In small lemur groups of 10 individuals or less, instead of summing strength of the top three connections, we used only the strongest two or one, depending on the average number of above average strength connections individuals of the group had (top one RedFrL1, top two all sifaka groups). As social integration metrics, we used (8) individual strength, e.g., the sum of all DSI values an individual shared, equivalent to the CSI used in Silk et al.

(2003), (9) the number of connections an individual had (individual degree), and several counts (metrics 10–14) of the number of weak ties all excluding zero (McFarland et al. 2017). These were (10) all ties with a DSI<1 or smaller than the mean corrected grooming or proximity time following (McFarland et al. 2017; Silk et al. 2018) and all ties weaker than (11) the 1st, (12) the 2nd, and (13) the 3rd quartile of tie-strength across all connections in the group, as well as (14) those weaker than the 0.9 percentile, because some previous research differentiated the strongest top 10 % of ties from the rest (Silk et al. 2006b). All data manipulations for these analytical steps were done in Microsoft Excel. We measured indirect connectedness as (15) weighted Eigenvector centrality which increases not only with the strength of an individual's direct connections but also with the strength of all its partners' connections and (16) weighted betweenness, i.e., the weight of all the shortest path between any two individuals in the network that go through the individual of interest. These two metrics have been chosen for their frequent use in studies linking sociality to fitness (Ostner and Schülke 2018). Eigenvector centrality integrates node strength with the strength of neighboring nodes and measures to which degree an individual's own connections give indirect access to individuals one step away in the network (Cheney et al. 2016). Betweenness grasps to which extent an individual connects otherwise unconnected parts of the network with benefits accruing from increased information flow (McFarland et al. 2017) or the ability to tap into different coalition networks (Gilby et al. 2013); see discussion for applicability to small networks. Betweenness and Eigenvector centrality were calculated for weighted networks where

tie weight represented the DSI, the duration of grooming per hour of observation, or the duration of time spent in close proximity per hour of observation. We used the function betweenness in the igraph package version 1.2.4.1 (Csárdi and Nepusz 2006) after calculating the inverse of all matrix values, as igraph interprets weights as distances in these functions, and the function evcent to calculate Eigenvector centrality in the sna package (Butts 2016), both in R studio version 3.6.3 (RStudio Team 2020) and R version 3.6.3 (R Core Team 2020).

Covariation patterns

For every group of animals, we then ran all pair-wise Pearson correlations of metrics across individuals to assess their covariation within a network in Statistica 13 (StatSoft Europe, Hamburg, Germany). We present the mean of directional correlation coefficients across all study groups as a central tendency and the standard deviation across all groups as a descriptor of disagreement between patterns in different groups visualized in heatmaps. We used hierarchical clustering to organize these heatmaps and visualize groups of sociality metrics with similar correlation coefficients by using the complete-linkage clustering method on Euclidean distances implemented in the pheatmap package (Kolde (2019)). Hierarchical clustering is useful for summarizing group structure within multivariate data sets, such as the one explored here (Legendre and Legendre 2012). The complete linkage clustering method allows incorporating all data, without a priori classification of clusters and is often applied in ecology, where one wishes to delineate clusters with clear discontinuities (Legendre and Legendre 2012). We also used the packages ggplot2 (Wickham and Chang 2016) and reshape2 (Wickham 2007) to manipulate and visualize data in R version 3.6.3. (R Core Team 2020).

To give an example, we constructed the grooming duration network for red-fronted lemur group J with ties representing the duration of grooming per hour of observation of either partner and then calculated for each of the 10 adult and juvenile group members their number of grooming partners, the strength across all of their grooming relationships, their betweenness in the grooming network, and so on for all 16 metrics. We were interested in how these metrics covary in a group. So we built a 16×16 matrix of all metrics over all metrics and populated it with the Pearson correlation coefficients between pairs of metrics, e.g., the correlation across individuals of grooming degree and grooming strength, of grooming degree and betweenness, of grooming strength and betweenness, and so on. The procedure was repeated with grooming duration networks for all groups. Then for each cell in the 16 × 16 matrix of metrics, we summarized data across groups to yield the average or standard deviation of the correlation between grooming degree and grooming

strength, for example. In a final step with hierarchical clustering, we assessed how similar sociality metrics were in their covariation with the other metrics.

Results

Covariation among metrics and clustering into concepts

After reporting for each index (DSI, grooming time, time in proximity) separately all pair-wise correlations of the 16 metrics across individuals in a group in a correlation matrix, we took the mean and standard deviation for each correlation coefficient across the 15 groups and plotted it in a heat map that was ordered by hierarchical clustering of similarity in covariation (Fig. 1). The clustering revealed that metrics did not all fall clearly into the three concepts we proposed. One big cluster comprised all of the social bonding metrics which were highly correlated among each other on average (mean ± SD of $r = 0.8 \pm 0.11$ for all indices) with only one, two, or three coefficients (out of 21) below 0.6 for the DSI, grooming, and proximity indices, respectively (Fig. 1) and only very little variation across groups, i.e., very little disagreement around the central tendency of strong covariation (mean of SD of $r = 0.04, 0.05, 0.05$ for data in Fig. 1). The sum of the strength of all connections an individual had (equivalent to the CSI in Silk et al. (2003)), which was construed as a measure of social integration, fell deep into the bonding cluster irrespective of which index (DSI, grooming, or proximity) we used to quantify sociality. Likewise, the two metrics of indirect connectedness did not form their own cluster. Betweenness and Eigenvector centrality fell into the social bonding cluster, albeit in different subclusters, highlighting the fact that betweenness and Eigenvector centrality were only moderately correlated with each other in the DSI network ($r = 0.6$) and the proximity network ($r = 0.5$).

Beyond the social bonding cluster, the second large cluster comprised all the different counts of weak ties with their different thresholds for defining weak versus strong. Pairwise correlations within this social integration cluster were weaker than in the social bonding cluster: mean ± SD of $r = 0.66 \pm 0.15$ for DSI or grooming and 0.62 ± 0.17 for proximity networks.

The overall number of partners an individual had (network degree) fell right in between the two large clusters and had no strong correlations with any single measure except the number of weak ties with a threshold at 90% weakest, suggesting it represents an independent dimension of variation in sociality.

Comparison between sociality indices

Comparison of covariation patterns between the three indices (DSI, grooming duration, and time spent in proximity) revealed similarities and differences. Networks built from the three indices are similar (a) in how the social bonding cluster comprises also overall strength as well as the indirect connectedness metrics and (b) in how number of partners falls between this cluster and the weak tie cluster of social integration. What differs depending on index is the covariation between clusters. In grooming networks, the social bonding metrics and the counts of weak ties are uncorrelated, whereas they are on average weakly to moderately negatively correlated in proximity networks. This discrepancy becomes more tangible if species are treated separately (Supplementary Material S1–S3). Clustering of metrics derived from the grooming network varies less between species, and few pair-wise between-cluster correlations reach a moderate strength. In contrast, the correlation matrices derived from proximity networks differ between species, with moderate (RedFrL) to strong (Chimp, Sifaka) negative correlations of metrics between clusters compared to correlations close to zero in both macaque species. All but one group of lemurs and chimpanzees exhibited complete proximity networks, i.e., every individual was associated with every other individual of the group to some degree, which binds together counts of strong and weak ties with the same threshold. The grooming networks are less dense, providing a degree of freedom in these correlations because proportions of weak and strong ties do not have to add up to one.

More specifically, network density, that is the proportion of realized pair-wise connections between individuals out of all possible connections, was high at 0.90 ± 0.15 (mean $\pm$ SD) in proximity networks and at 0.89 ± 0.13 in DSI networks and lower in grooming networks at 0.64 ± 0.22. Across groups, network density was not correlated with sampling effort measured as hours of focal animal sampling per individual in networks built from DSI, grooming, or proximity time ($0.02 < r < 0.09$, $0.75 < p < 0.94$). Thus, under-sampling is unlikely to explain between-group variation in network density in this data set (Macdonald and Voelkl 2014; Ostner and Schülke 2018). Network density decreased strongly with group size in grooming ($r = -0.70$, $p = 0.004$) and proximity ($r = -0.84$, $p = 0.001$) and less so in DSI networks ($r = -0.46$, $p = 0.09$).

Group size also predicted the number of weak and strong ties individuals formed in DSI and proximity networks (Fig. 2). The effect size for weak ties was twice as large as for strong ties (slopes 0.4 vs. 0.2), reflecting the strongly skewed distribution of tie strength perhaps resulting from social selectivity (Ostner and Schülke 2018). In the grooming network, the number of weak ties was less closely associated with group size, but the number of strong ties increased at a rate of 0.2 with every additional adult in the group.

Discussion

This study was motivated by a need for an agreement on how to quantify sociality, i.e., individual position in the affinity and affiliation structure of a group. Past studies have measured within-group, inter-individual variation in sociality using different indices of affiliation and affinity as well as several different metrics that quantify different concepts of sociality: social bonding, social integration, and indirect connectedness. Reviewing our results on systematically collected data from representatives of all independent clades of group-living primates together with published work, we discuss below how similar metrics of the same sociality concept are and to what extent the concepts may be overlapping. We further discuss results across sociality indices and a number of methodological issues.

Robustness of sociality concepts

We found that all metrics used to date to quantify social bonding are highly correlated with each other and with overall strength (sometimes construed as a social integration metric). These correlations were largely independent of the index used to build the network. Thus, studies that employed any of these indices and metrics (whatever the strong-tie threshold) may have assessed one and the same biological phenomenon when relating these metrics to fitness outcomes, which points to its generality. This conclusion echoes previous results of strength of all ties and the strength of only the three strongest connections per individual both being correlated to fitness components in DSI networks of yellow baboons, *Papio cynocephalus* (Silk et al. 2003; Archie et al. 2014; Campos et al. 2020), Assamese macaques (Schülke et al. 2010; Ostner and Schülke 2018), and rhesus macaques (*M. mulatta*) with a marginally significant effect of overall strength (Ellis et al. 2019). In contrast, the number of partners was not generally closely correlated with the social bonding metrics. Thus, there is no broad support for a trade-off between number and average strength of ties, which would have resulted in strong negative correlations between number of partners and strength metrics (Archie et al. 2014). Our data do not suggest quantity vs. quality trade-offs at other strong tie cut-offs either.

The covariation between social bonding and indirect connectedness metrics observed in this study seems less generalizable. Betweenness and Eigenvector centrality both quantify how an individual is indirectly connected via its direct social partners; both are weighted by the strength of

Correlation coefficient
−1 −0.5 0 0.5 1

Concept
social integration social bonding indirect connectedness

Standard deviation
0 0.2 0.4 0.6 0.8 1
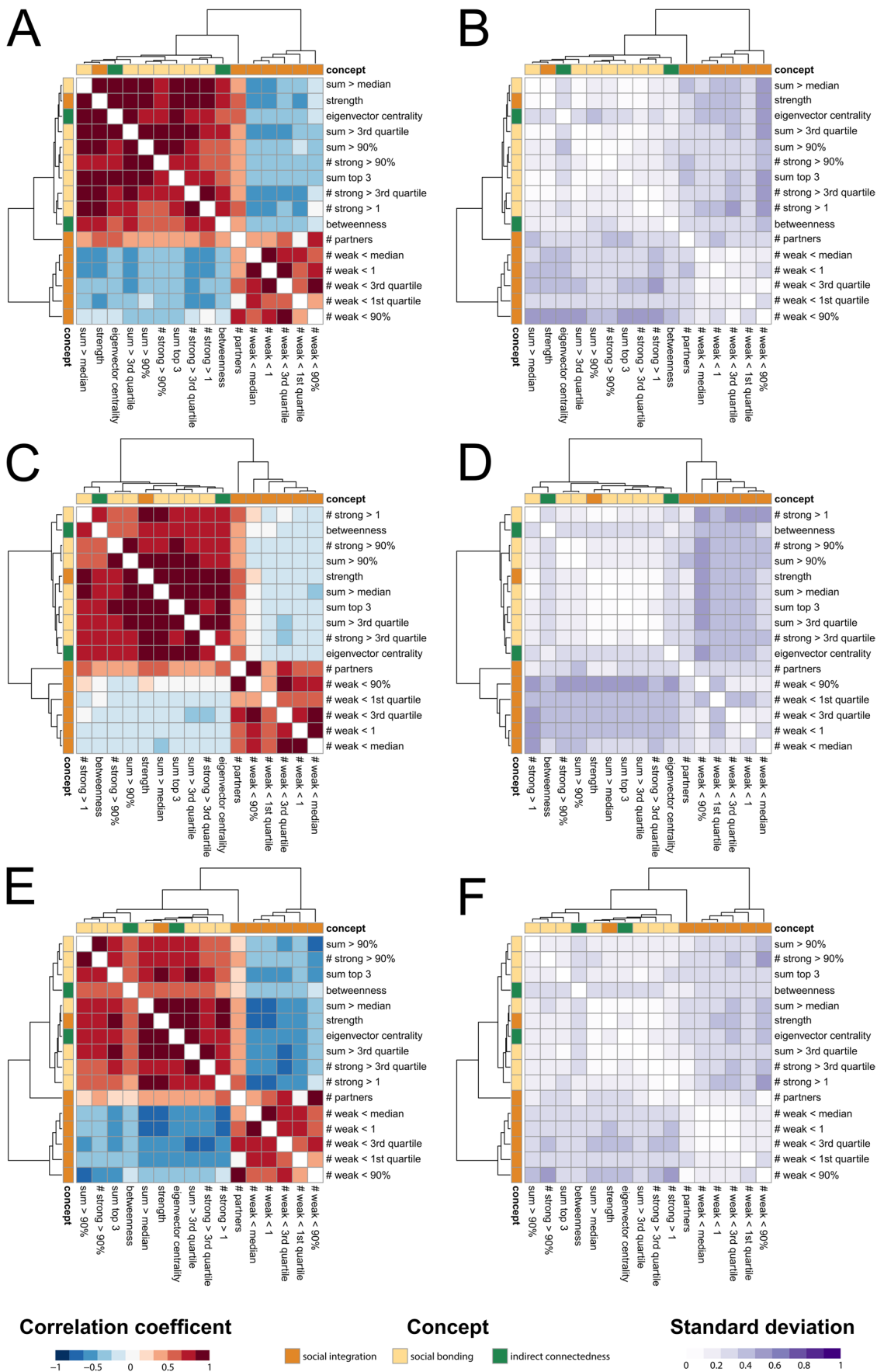
◄**Fig. 1** Hierarchical clustering by similarity in covariation of sociality metrics for three indices: DSI (**A**, **B**), grooming duration (**C**, **D**), and time spent in proximity (**E**, **F**). Plotted are the means (**A**, **C**, **E**) and their standard deviation (**B**, **D**, **F**) across 15 groups of within-group pair-wise correlations of metrics. Clustering in standard-deviation plots is copied from the respective mean plot to facilitate cross-reference

connections to those direct partners which will be the reason why they fell in the social bonding cluster. Despite their moderate to high dyadic correlation coefficient, covariation patterns of betweenness and Eigenvector centrality did not cluster closely together in our summary statistics (Fig. 1) or species accounts (S1–S3). In previously published rhesus macaque DSI networks, the metrics employed here were less strongly correlated between social bonding and indirect connectedness, and indirect connectedness was not related to a fitness component (Ellis et al. 2019). In wild Barbary macaques, strength in an affiliation time network
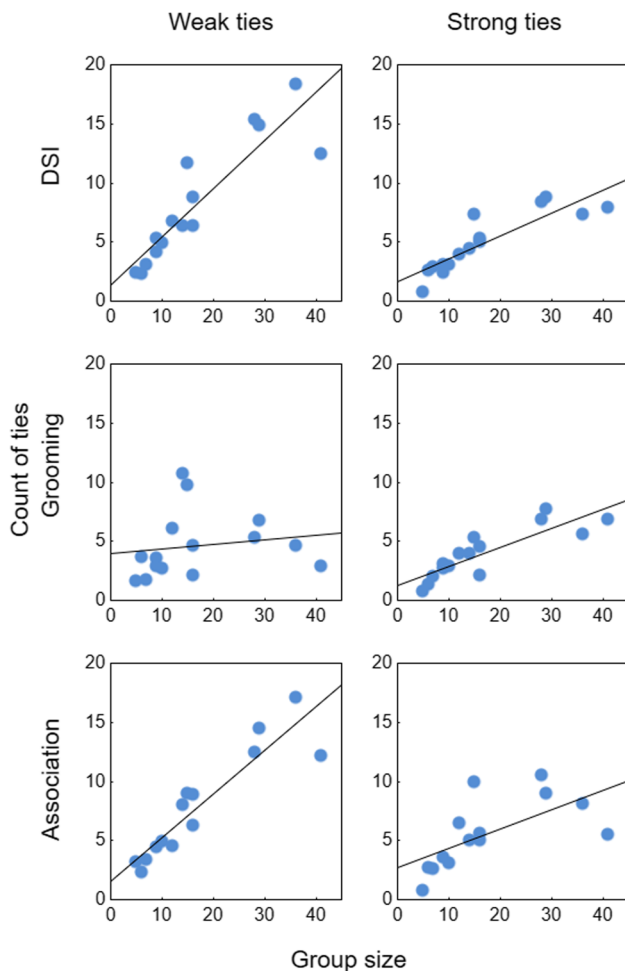
Fig. 2 The average count of weak ties across individuals in a group (with mean tie strength as a threshold) increases more steeply with group size than the count of strong ties in proximity and DSI networks but not in grooming networks. Data points are means across individuals of a group

was positively correlated to both Eigenvector centrality and betweenness (Lehmann et al. 2016) more closely matching our results. Likewise, both Eigenvector centrality in a DSI network (Cheney et al. 2016) and the strength of the strongest ties (Silk et al. 2009) predicted a fitness component in the same chacma baboon (*Papio ursinus*) group; betweenness in the same network was negatively instead of positively related to average strength and thus indirectly also negatively correlated to Eigenvector centrality (Cheney et al. 2016), but we suspect that weights have been interpreted as distances which, if corrected, could result in positive correlations between betweenness and Eigenvector centrality also in that study. Outside of primates, in juvenile bottlenose dolphins, *Tursiops* sp., strength in a proximity network was neither correlated to betweenness nor Eigenvector centrality (Stanton and Mann 2012) and neither were strength and betweenness in affiliation networks of yellow-bellied marmots, *Marmota flaviventris* (Wey and Blumstein 2012; Wey et al. 2013).

For a conclusion across studies, it is important to realize that betweenness and Eigenvector centrality can only capture meaningful variation in dense networks, if tie weights are considered in this study instead of just using binary networks of the presence or absence of a connection (Lusseau et al. 2008; Kasper and Voelkl 2009). But even if tie weights are taken into account, the discrepancies between studies described above concerning whether indirect connectedness and social bonding capture different dimensions of sociality may be explained by remaining variation in network density and modularity, i.e., global network characteristics (Sosa et al. 2021). If networks are generally rather dense, like in most primates (Kasper and Voelkl 2009), the opposite ends of the network will be connected to each other via many different routes. As a consequence, there will be little variation between individuals in how important they are in connecting these ends. If the network is more modular instead, members of different modules are connected only by one or a few routes, and betweenness will vary much more between individuals as is the case in bottlenose dolphins and yellow-belied marmots. It is also a characteristic of most primate social networks that they are locally highly clustered (Kasper and Voelkl 2009), so that the partners of two closely connected individuals are also closely connected (e.g., within matrilines). The stronger this pattern is, the less informative will be the Eigenvector centrality metric. Thus, while social bonding can be compared across groups of different sizes and structure, the information content of indirect connectedness metrics will depend more on network level social structure (e.g., density, local clustering, modularity) which hampers their applicability in comparative studies.

Beyond effects of social bonding and indirect connectedness, it has been established that another aspect of social integration, the number of ties and particularly of weak

ties may affect health (VanderWaal et al. 2016) and fitness (McFarland and Majolo 2013; McFarland et al. 2017). In this study, counts of strong ties fell into the social bonding cluster and counts of all ties in between clusters. If network density was low enough to permit some degree of freedom, counts of weak ties did not (or only weakly) correlate with metrics of social bonding. The same dissociation was found in one (McFarland et al. 2017) of two chacma baboon studies (Silk et al. 2018) and in rhesus macaques (Ellis et al. 2019). Both of these studies also found social bonding and counts of weak ties to (independently) predict fitness components. Thus, counts of weak ties may capture an independent dimension of variation in affinity and affiliation that is not well represented by other metrics. This may be true only for somewhat scarce networks (Silk et al. 2018); if networks are (nearly) complete, counts of weak ties are the residual of counts of strong ties to all ties. The function of such weak ties has been proposed to accrue from the indirect connections they provide (Granovetter 1976; VanderWaal et al. 2016; McFarland et al. 2017). Yet, counts of weak ties were not strongly correlated to measures of indirect connectedness, neither in this nor the rhesus macaque study cited above. The count of weak ties may, therefore, be best construed as an index of the tolerance towards and from group members that are either not important enough to form a closer relationship with or where time or other constraints prohibit the development of stronger ties. Enhanced tolerance may benefit the individual by increasing access to safe positions in the group, to thermo-regulation huddles, to social learning opportunities, and because it allows the individual to more freely move though the group, enhanced tolerance may allow the individual to more freely follow its own needs (Ostner and Schülke 2018; Sosa et al. 2021).

Comparisons between sociality indices

Differences in network density may also be responsible for the moderate differences in covariation patterns depending on the choice of index. The dissociation between social bonding metrics and social integration as captured by counts of weak ties is most pronounced in grooming networks, which can be attributed to their lower density. Therefore, the grooming network provides a more nuanced picture with at least two different dimensions capturing inter-individual variation in affiliation. The complete proximity networks of chimpanzees and many lemur groups caused dependencies in the data. DSI networks maintained some, but not all of the dependencies, because proximity was not a component in all DSI constructs. Reasons for every group member to be spatially associated with every other at least once over the course of 1 year of sampling are small group size in lemurs (5–10) and a measure of spatial proximity that was unique to chimpanzees. Owing to their social organization

with high fission-fusion dynamics, i.e., frequently changing subgroups (Lehmann et al. 2007), for chimpanzees, we used an association index that captured membership in the same subgroup instead of scoring proximity as time spent in close proximity of 1 or 1.5m as in lemurs and macaques. As a consequence of network completeness, variation in sociality was collapsed into one dimension in affinity networks of red-fronted lemurs, sifakas, and chimpanzees. It remains to be shown whether patterns of chimpanzee affinity if measured at a smaller scale can be characterized along several independent dimensions.

The covariation patterns of metrics derived from DSI networks were least affected by sampling and group size effects and suggest different dimensions of sociality can be extracted with metrics from different concepts. Affinity networks need to be used with care, because in species forming closed groups, they may saturate quickly if sampling is dense. It is important to note that affinity is not strictly speaking a dyadic behavior that is exchanged between two individuals; both may be close to each other because they are attracted by a third individual or the same food resource. The fact that patterns of direct contact affiliation correlate well with patterns of close spatial proximity in the many species for which composite sociality indices have been constructed suggests, however, that attraction to a third party introduces noise but does not generate independent patterns of proximity. The same may not be true though for societies with high fission-fusion dynamics.

Methodological considerations

In the "Methods" section, we provided guidelines for the construction of composite sociality indices including pairwise correlation tests between all components and data density assessments for every new data set. The DSI is a data reduction technique, and since it integrates more information, it is affected less by outliers in one component, e.g., if a dyad grooms very often but bouts are generally short, the duration brings down the outlier in frequency, or if a dyad associates a lot but does not groom, the latter will bring down the composite index.

Directly comparing sociality metrics between groups and species could be hampered by sampling issues, differences in fission-fusion dynamics, and variation in global network topography. If observational sampling is scarce, and the distribution of relationship strength highly skewed as is typically the case (Silk et al. 2006a; Kalbitz et al. 2016; McFarland et al. 2017), observed network density may be low with many of the possible ties not being realized, simply because many dyads that interact only rarely have not been observed in proximity or contact (Lusseau et al. 2008). Our comparisons of network density and observation hours per individual across groups suggest adequate sampling in this

study. Yet, the larger the groups, the sparser the networks were, because every added individual added only 0.4 weak and 0.2 strong ties per group member in proximity and DSI networks. These patterns either suggest time constraints (Dunbar 1992) imposed by foraging on dispersed resources (Henzi et al. 1997), constraints on social cognition (Dunbar 1998), or network modularity increasing with group size (Kasper and Voelkl 2009). When released from time, space, and energy constraints as in captivity, macaques in small to medium-sized groups (7–25) do not show an increase in affiliation network density with increasing group size (Sueur et al. 2011b).

Chimpanzee fission-fusion dynamics further complicate the quantification of grooming relationships. Here we used the raw grooming counts and durations and controlled them for the combined observation time for the two individuals involved to standardize the procedures across species. Studies on chimpanzee grooming behavior typically control instead for the opportunity to groom, i.e., for the observation time that both partners spent in the same party (Bray and Gilby 2020). This seems problematic if the adaptive value of close ties results from agonistic support or any other mechanism that requires proximity, because dyads that are almost always traveling in the same party and groom a lot on all accounts will have proximity-corrected grooming indices that are as high as dyads that are rarely in the same party but always groom if they do (which is rare in absolute terms). That the latter dyads exist is suggested by the fact that grooming is not correlated to party association in two of three chimpanzee groups in this study. This is not surprising because two individuals may travel in the same party for a number of different reasons other than their dyadic relationship. But if association is required for generating fitness benefits, corrected grooming indices may not capture fitness-relevant aspects of affiliation. In support of this notion, both pure proximity metrics and grooming metrics uncorrected for proximity were strongly correlated with male dominance rank trajectories in a study on eastern chimpanzees, whereas metrics derived from grooming corrected for time spent in the same party were much weaker predictors of future social status (Bray et al. 2021).

It is important to note that this study treated all adults and their combinations into dyads the same. If one seeks to link sociality to fitness, this may be problematic for two reasons: relationships among different classes of individuals may have different functional significance (Ostner and Schülke 2018; Thompson 2019), and relationship metrics calculated across classes of dyads may therefore not predict fitness outcomes very well. Furthermore, different classes of dyads (e.g., female-female versus male-female dyads) may on average interact at very different rates but within-class variation may equally affect fitness outcomes for the individual. If one function of affiliative connections is

mutual support in agonistic conflicts (Schino 2006), in many species, females would benefit more from bonding with a larger male supporter compared to a female (Haunhorst et al. 2017). For this function, we would, therefore, expect variation across females in male-female relationships to have a much stronger effect on fitness outcomes than variation in female-female relationships. Yet, in our analyses, we have integrated dyadic relationship measures across all types of dyads. If average interaction rates or durations are much lower for males than for females as, for example, in Barbary macaques (Müller-Klein et al. 2019) but not, e.g., in yellow baboons (Campos et al. 2020), the integration of dyadic relationships at the individual level as exercised here will wash out the relationships with males, if one does not weigh them differently than the relationships with females. Furthermore, it is possible that pronounced differences between classes of dyads in interaction frequencies make all affiliative behavioral measures (proximity, grooming, body contact) highly correlated among each other across the entire network which could potentially mask that these behaviors are not correlated well within class.

We have limited our analyses to just two affiliative contact behaviors and one measure of affinitive behavior. We neglected agonistic behavior including agonistic support (Crockford et al. 2013), trading like food sharing (Samuni et al. 2018), or tolerance-enhancing behaviors like triadic interactions with infants (Kalbitz et al. 2017). Integrating these additional behaviors has pros and cons: it allows identification of additional dimensions of variation in sociality or types of social relationships (Fischer et al. 2017a), but it also conflates assessment of relationship quality with the adaptive benefits individuals gain from their partners be it support, food, or safety (Ostner and Schülke 2018). In following our aim to assess the generality of covariation patterns among different sociality metrics, we chose only behaviors that were shared among the species we study.

Generalizability of results

Results of this study were rather robust across different taxa of non-human primates. It seems likely though that species living in different social organization types will form social networks with different characteristics where sociality metrics cluster in different ways. Indirect connectedness might have larger fitness consequences and be more different from social bonding where groups are more modular, e.g., in hierarchically structured social organizations like that of guinea baboons (Fischer et al. 2017b). In such cases, information or disease transfer might occur primarily through individuals with high degrees of indirect connectedness. In our study, direct and indirect connectedness was strongly correlated. A possible explanation for this could be phenotypic assortment (Wolf et al. 1999), i.e., that individuals with more and

overall stronger bonds tend to be connected with individuals that themselves have more and stronger bonds and thereby increase their indirect connectedness. Another aspect of social organization that may hold a special place for indirect connectedness might be more open societies where group membership is more fluid than in the species studied here (Sosa et al. 2021). In animal societies with open groups like some equids (Sundaresan et al. 2007), giraffes (vanderWaal et al. 2016), or Tasmanian devils (Hamede et al. 2009), social networks will be much sparser so that indirect and direct connectedness might possibly be less strongly correlated because less central individuals could share more connections to individuals outside of groups. To our knowledge, this still remains to be tested.

Summary and recommendations for future studies

In summary, we found the strength and number of strong ties to have a disproportionately large influence on overall tie strength and indirect connectedness. Due to the strong covariation between these aspects of sociality, it will be difficult to disentangle their independent effects on fitness correlates. It seems possible that they are all the consequence of variation in sociability— variation in the tendency to seek proximity and engage affiliatively with any partner—with indirect connectedness emerging in the closed system that is a social group or simply being a better representation of true sociability given sampling (Firth et al. 2017). It will be easier to assess the independent effects of the number of weak ties and of overall number of partners (at least if networks are moderately sparse), but in contrast to the number of partners (Ostner and Schülke 2018), conceptual work is required to explain how weak ties will affect fitness. Our discussion of the sociality-fitness link highlights that the choice of metric in an empirical study always should be dictated by the research question and the theory it is testing including mediating mechanisms (Ostner and Schülke 2018; Sosa et al. 2021; Weiss et al. 2021).

In cases with several mediating mechanisms that might link different aspects of sociality to an outcome variable or cases where the mediating mechanisms are obscure, we recommend to assess social bonding by quantifying the strength or number of strong ties, consider the possibly independent effects of indirect connectedness especially in open societies and sparse networks, and measure the two aspects of social integration by counting all ties and only the weak ones separately. If networks are complete or near complete, counts of strong and weak ties cannot capture independent aspects of sociality and should not be interpreted that way. With association or proximity usually being more frequent than contact and social interaction, association networks or composite sociality indices including proximity are more prone to this problem, whereas the biggest issue with interaction

networks will be under-sampling where ties that exist and are relevant to the animals are not observed. Comparative work will be required to understand how covariation among sociality metrics depends on global network characteristics in empirical networks resulting from variation in animal social systems.

Declarations

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