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Disparate social structures are underpinned by distinct social rules across a primate radiation

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AUTHOR CONTRIBUTIONS

J.A.F., J.M.K., and J.B.S. designed research; J.A.F., S.C.A., E.A.A., M.E.A., A.B., J.C.B., T.J.B., A.J.C., M.J.E.C., K.L.C., C.C., G.C., F.D.P., D.F., J.F., J.P.H., E.H., A.L.F., J.L., A.L, G.M.M., A.M., B.M., M.P., C.R., I.A.S-C., R.M.S, N.S-M., L.S., F.T., J.T., A.H.W., R.M.W., J.M.K., and J.B.S. performed research; J.A.F. analyzed data; J.A.F. and J.B.S. wrote the paper with feedback from all authors.

COMPETING INTEREST STATEMENT

The authors declare no competing interests.

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This PDF includes:

Main Text
Figures 1 to 4

ABSTRACT

Over six decades of research on wild baboons and their close relatives (collectively, the African papionins) has uncovered substantial variation in their behavior and social organization. While most papionins form discrete social groups (single-level societies), a few others form small social units nested within larger aggregations (multi-level societies). To understand the social processes that shape this variation, a more systematic, comparative analysis of social structure is needed. Here, we constructed a database of behavioral and demographic records spanning 135 group-years across 13 long-term papionin field studies to (i) quantify variation in grooming network structure, and (ii) identify the factors (e.g., sex, kinship, and social status effects) that underlie these differences. We detected considerable variation in grooming network structure across the papionins, even within the classic single-level societies. The papionins could be best divided into three broad categories: single-level *cohesive*, single-level *cliquish*, and *multi-level*. The cohesive single-level societies formed networks that were dense, moderately kin-biased, and weakly rank-structured, while the cliquish single-level societies formed networks that were relatively modular, highly kin-biased, and more strongly rank-structured. As expected, multi-level networks were highly modular and shaped by females' ties to specific dominant males but varied in their kin biases. Taken together, these data suggest that: (i) discrete typologies obscure variation in social structure; and (ii) similarities in social structure are sometimes, but not always, shaped by similar social processes.

SIGNIFICANCE STATEMENT

Do all primate groups fit the same social mold? While factors like kinship and dominance shape the social lives of many of our close relatives, it remains unclear how their effects differ across species. Using a new database representing decades of field research, we found that baboons and their close relatives fell into one of three general patterns: one in which groups were cohesive and only somewhat nepotistic (i.e., kin- and rank-biased), another in which groups were more cliquish and nepotistic, and a final pattern in which groups were divided into clusters centered on dominant males. Distinct primate societies may thus reflect differences in the strength of females' social biases towards kin and the degree of males' social influence.

MAIN TEXT

INTRODUCTION

Behavioral ecologists have long sought to identify the selective pressures that shape the evolution of sociality across mammals (1–3) and primates in particular (4–6). Theoretical and empirical work both suggest that extrinsic factors, such as the distribution of foods and the intensity of predation risk (7–10), shape the size, composition, and cohesion of social groups (i.e., social organization: 11), while intrinsic factors, such as kinship, reciprocity, and mate competition (12–15), influence the tenor, frequency, and stability of interactions within groups (i.e., social structure: 11). On the whole, these theoretical frameworks have been moderately successful in linking ecology with the size and composition of social groups (16, 17), but less successful in predicting the emergence of dominance hierarchies, kin structure, and differentiated relationships within groups (reviewed in 18, 19). This is partly because comparative research has historically lacked the fine-grained data necessary to quantify variation in the internal structure of social groups. However, individual-based field studies (20), collaborative science initiatives (21), and social network methods (22) have increasingly facilitated and encouraged the construction of comparative social interaction databases (e.g., MacaqueNet: 23, DomArchive: 24, Animal Social Network Repository: 25, reviewed in 26).

Here, we have compiled a new database of behavioral and demographic data from 13 long-term field studies of baboons and their close relatives: collectively, the African papionins (**Figure 1**). The Comparative Analysis of Papionin Societies (CAPS) database is collaborative, standardized, and designed to explore links between ecology, demography, and social structure. The papionins are an ideal lineage for assessing the processes that shape social structure because they have been studied extensively in the wild over the last 60 years, owing in large part to their use as model systems in human evolutionary research (27–31). This research has uncovered substantial variation in ecology, dietary niche, and social organization across the clade (reviewed in 32). While most papionin species form single-level societies in which individuals freely socialize with all co-resident group members, a few form multi-level societies in which small, one-male reproductive units are embedded within large, nested societies (33). Multi-level societies have evolved at least twice in the papionins (34), once in geladas (*Theropithecus gelada)* and once or twice in baboons (*Papio* spp.).

The single-level (mangabeys, mandrills, and most baboons) and multi-level papionins (Guinea baboons, hamadryas baboons, and geladas) show broad variation in their group sizes, dispersal patterns, competitive regimes, and resulting social strategies (32, 35–37). In the single-level societies, females typically remain in their natal groups and comprise the core of the social group, developing strong relationships with their maternal kin and forming matrilineal dominance hierarchies in which related females occupy adjacent ranks (38–42). However, preliminary comparative data suggest that these patterns may vary in their strength across the single-level species (43), perhaps because kinship and rank play more important roles in harsher competitive regimes. By contrast, in multi-level hamadryas and Guinea baboons, females do not stay in their natal units (44, 45), limiting opportunities for females to form lasting ties to their maternal relatives. Female dispersal is wholly voluntary in Guinea baboons but not in hamadryas baboons, in which females are forcibly transferred between units by males via ‘takeovers’ (46). In multi-level geladas, females remain in their natal units, form matrilineal hierarchies, and develop strong kin bonds (47, 48). Despite these differences, females form strong relationships with dominant, reproductive males in all of the multi-level societies (49–51). Between-sex relationships are also common in the single-level papionins but vary in their strength and durability (43, 52–54), perhaps due to differences in the intensity of male-male mating competition (55), the degree of female mate choice, and the benefits individuals can derive from these relationships (15, 56).

Given this wide variation in social structure, there may be areas of subtle overlap between the single- and multi-level societies that warrant further exploration. For instance, Kinda baboons and mandrills both form groups that have been likened to multi-level societies, as female-male

relationships play a more central role in group structure (Kinda baboons: 53), and groups can become very large and putatively clustered (mandrills: 57, but see 58). Within-species variation may also provide insights into how and why groups become modular (59). While single-level baboons primarily form stable multi-male, multi-female groups, they sometimes fracture into small one-male groups that resemble the one-male units seen in multi-level societies (60, 61, reviewed in 62). These small one-male groups are most commonly found in chacma baboons inhabiting marginal, high-altitude environments (61) but have been observed elsewhere in the single-level papionins (63, 64). In combination, these data indicate that the single-level and multi-level societies may each comprise a mosaic of concordant and distinct social patterns. Standardized behavioral data are needed to capture this fine-grained variation in the structure of papionin social groups, place the single-level and multi-level societies along key axes of variation, and determine whether similar social topologies emerge from the same social "rules."

In this inaugural study, we use social network methods to capture grooming interaction patterns, which have been long used to quantify the strength and tenor of primate social bonds (65). In particular, we (i) capture variation in grooming network structure across the papionins; (ii) measure the strength of nepotism, rank-related effects, and shared-male preferences on female-female grooming relationships; (iii) quantify the impact of dominance rank on female-male relationships; and (iv) identify links between the strength of these female-female and female-male grooming biases and network structure. These analyses provide the foundation for a more comprehensive synthesis of sociality and its structural underpinnings across the papionins. In constructing the CAPS database and documenting these patterns, we also lay the groundwork for further research targeting the ecological pressures and evolutionary forces that shape social structure in primates and social animals more broadly.

RESULTS

The CAPS database includes grooming data from 11 species across 13 sites, representing a total of 135 group-years of behavioral data from 28 distinct social groups (**Table S1**). When aggregating data at the group-level for the multi-level societies, we used the party for Guinea baboons, the clan for hamadryas baboons, and the band for geladas. Across the dataset, there was considerable variation in the size and composition of the sampled papionin networks (**Table S1**), as well as in the prevalence of grooming within and between the sexes (**Figure S1**). In general, female-female grooming was more prevalent than female-male or male-male grooming. Within female-male dyads, grooming from females to males typically exceeded grooming from males to females (except in Kinda baboons: **Figure S1**). Within our sample, male-male grooming occurred regularly in Guinea baboons and geladas (**Figure S1**). While male-male grooming is also prevalent among solitary and follower hamadryas males (66, 67), these interactions were not captured within the hamadryas dataset because it included only data from one-male units.

We used grooming data to construct weighted, directed grooming networks for each group-year within the dataset (n = 135, see **Figure 1a** for representative networks from each study site), including all adult and subadult individuals (>4 years for females, >7 years for males). Within each of these grooming networks, the strength of each relationship (i.e., network 'edge') reflected either (i) the proportion of observation time (in minutes or scan samples) that the dyad spent grooming or (ii) the number of times the dyad groomed during representative interaction sampling, adjusting for group-level differences in sampling effort (68). From these networks, we calculated two network-level measures: *density*, which reflects the proportion of all dyads that were observed grooming during that sampling period; and *modularity*, which reflects the extent to which a grooming network can be divided into discrete clusters via a random walk process (69).

Density and modularity varied widely across the sampled species (**Figure 1b**) but did not strictly map onto the phylogeny of the papionins. Intraclass correlation coefficients (ICC) indicate that roughly 20-35% of the variance in network structure could be attributed to phylogenetic position

(Density: $ICC_{Phylogeny}$ = 0.375, $ICC_{Species}$ = 0.437, $ICC_{Population}$ = 0.094; Modularity: $ICC_{Phylogeny}$ = 0.192, $ICC_{Species}$ = 0.244, $ICC_{Population}$ = 0.051). Thus, variation in network structure may also reflect species- and population-level differences in group composition, ecology, and derived social traits.

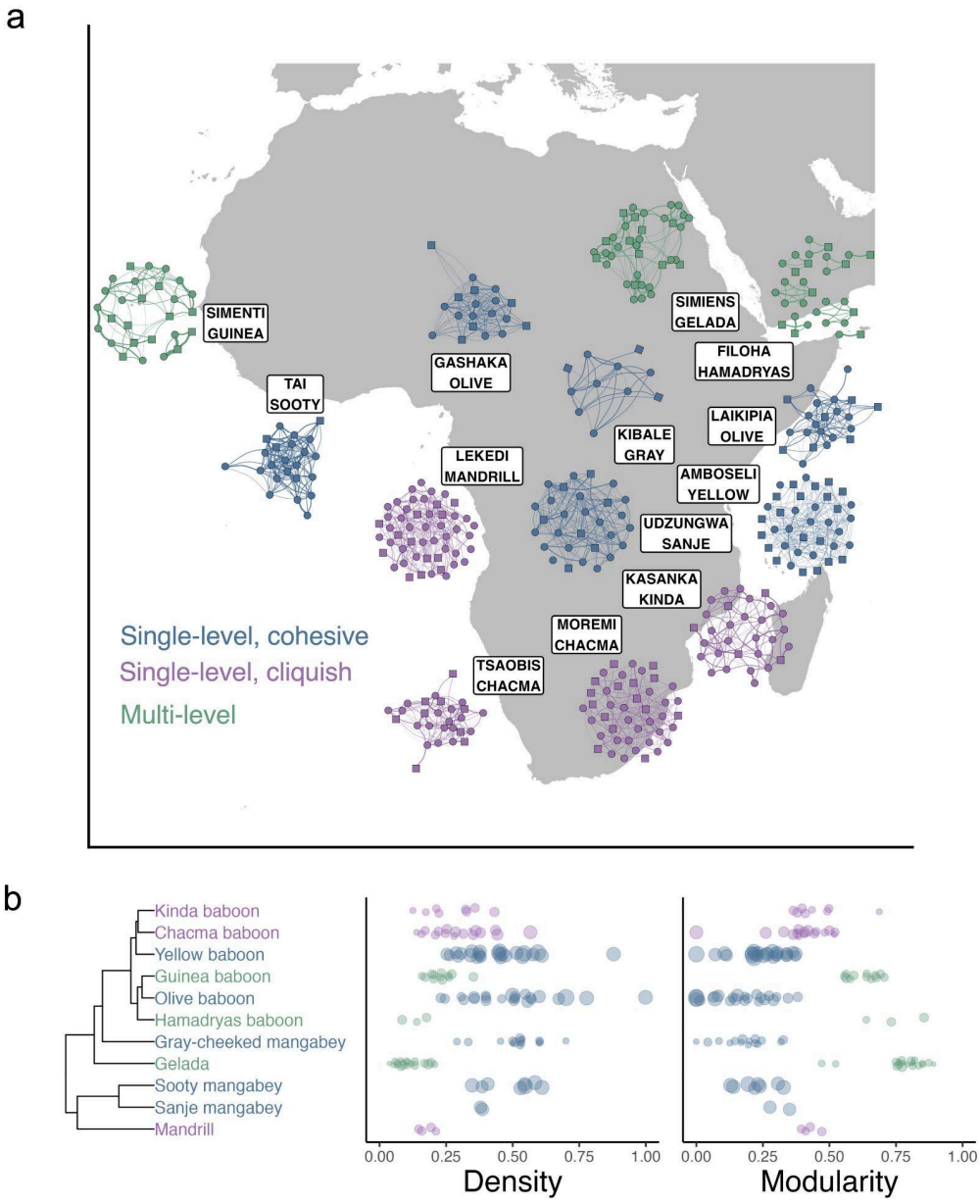

Figure 1. Grooming networks varied across the papionins. (a) Representative grooming networks across the papionins, provided over a map of collaborating field research sites. Within each network, circles indicate females, and squares indicate males. The width of each edge corresponds to the proportion of time or scans each dyad was observed grooming or the group size-adjusted rate of grooming interactions (undirected, to improve visibility). (b) The density and modularity of each grooming network within the sample, organized by species and provided alongside a phylogeny of the papionins, from Kuderna et al. (70). Here, the size of each point corresponds with the per capita sampling effort for that group-year's grooming network. In (a) and (b), each network and network measure are colored according to the social system types described in the Main Text (blue = cohesive, single-level; purple = cliquish, single-level; green = multi-level).

Papionin grooming networks vary as a function of network size and social system

We expected networks from species that form multi-level societies to be less dense and more modular than networks from species that form single-level societies. However, prior research (53, 58, 62), suggests that, even within the single-level societies, Kinda baboons, chacma baboons, and mandrills tend to form more modular groups than yellow baboons, olive baboons, and the three sampled mangabey species. Given this, there may be more granularity in social structure than that captured by single-level and multi-level categories. We therefore conducted additional analyses using an alternative three-factor predictor that divided the single-level societies into two *a priori* social structure categories: *cohesive* and *cliquish*. The cohesive category included olive baboons, yellow baboons, and both genera of mangabeys, while the cliquish category included Kinda baboons, chacma baboons, and mandrills. The third category included the three species that form multi-level societies (i.e., Guinea and hamadryas baboons, geladas).

To model the effects of social system type on network density and modularity, we constructed a set of phylogenetic regression models using 'brms' (71) in 'R' version 4.4.0 (72). We treated these network-level measures as beta-binomial and beta-distributed outcomes respectively, as they ranged between 0 and 1. In doing so, we modeled density as the number of dyads that groomed out of the total number of dyads that could have groomed. Across these models, the primary covariate of interest was social system type (i.e., either single-level vs. multi-level, or cohesive, cliquish, and multi-level). We included network size (i.e., the number of adults and subadults included in each network) as a covariate within these models because network-level patterns scale with group size both within (73, 74) and across species (75, 76). We also accounted for *per capita* sampling effort because networks become increasingly saturated as sample size increases (77). This is particularly crucial in our dataset, as researcher effort is often spread more thinly when studying larger social groups (68). We also accounted for species, population, group identity, and phylogenetic relatedness via random intercepts. For each metric, we constructed three models and compared their fits using leave-one-out cross-validation and Bayesian stacking: (i) a network size only model; (ii) a two-factor model, and (iii) a three-factor model.

When modeling density, the three-factor predictor did not substantially improve model fit over the two-factor predictor (model weights: two-factor = 0.38; three-factor = 0.35; group size only = 0.27). Thus, the single-level vs. multi-level dichotomy adequately captured variation in network density across the papionins. In general, smaller networks were denser than larger networks ($\beta_{GroupSize}$ = -0.43, 89% CI = [-0.52, -0.36], **Figure 2a**), and single-level networks were denser than multi-level networks ($\beta_{Multi\text{-}level}$ = -0.89, 89% CI = [-1.35, -0.45], **Figure 2b**). Interaction effects between network size and social system did not improve model fit, suggesting that these relative differences were consistent across all network sizes. Nevertheless, single-level and multi-level groups all reach very low density values at exceptionally large group sizes (**Figure 2a**).

In parallel with variation in network density, larger social networks tended to be more modular than smaller social networks ($\beta_{GroupSize}$ = 0.20, 89% CI = [0.12, 0.28], **Figure 2c**). Here, however, the three-factor predictor model provided an improved model fit over the two-factor model (model weights: two-factor = 0.32; three-factor = 0.60; group size only = 0.08). Cohesive societies were the least modular, cliquish societies were somewhat more modular ($\beta_{Cliquish}$ = 0.68, 89% CI = [0.30, 1.04]), and multi-level societies were by far the most modular ($\beta_{Multi\text{-}level}$ = 1.82, 89% CI = [1.43, 2.20], **Figure 2d**). As above, interaction effects between network size and the three-factor social system predictor did not improve model fit. To further validate this three-factor categorization, we generated a set of models in which papionin taxa were randomly assigned to one of three groups. The *a priori* categories that we adopted produced a better model fit than all other possible combinations of papionin taxa. Thus, this categorization scheme appears to capture true biological variation within the single-level species, even after accounting for differences in network size. We used this three-factor classification system in subsequent analyses, which focus on how female-female and female-male grooming patterns may underpin these structural differences.

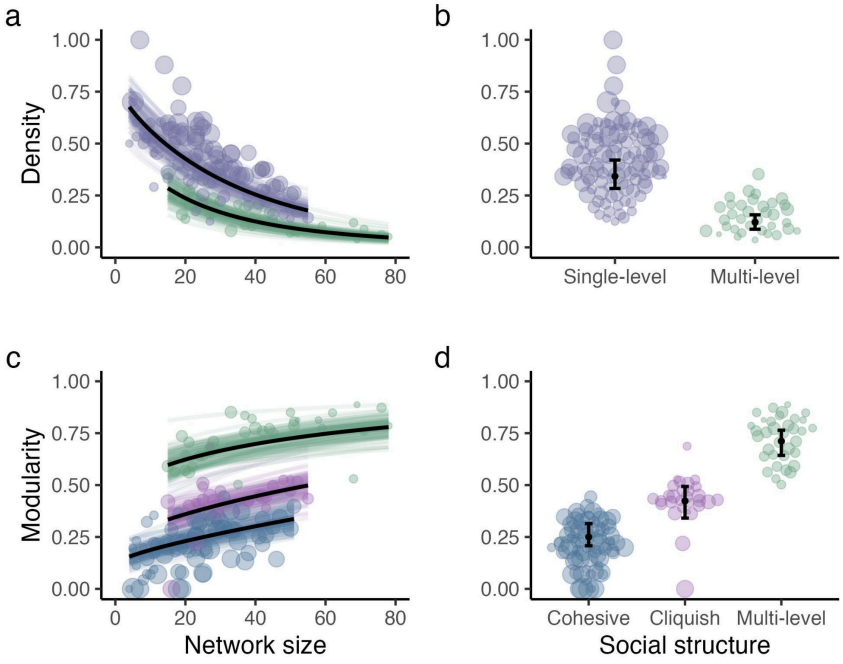

Figure 2. Network metrics varied as a function of network size and social structure type. (a,b) Density decreased with network size across the papionins and was generally lower in the multi-level societies. (c,d) Modularity increased with network size. Our analyses indicate that the papionins can be better divided into three distinct social structure types: cohesive, cliquish, and multi-level, in increasing order from the least to the most modular. Each point indicates the raw network value for that given group-year, and its size corresponds to its per capita sampling effort. In (a) and (c), each line represents one randomly drawn prediction from the posterior distribution.

Female-female grooming ties were variably shaped by kinship, rank, and shared male ties

To identify the patterns that produce this variation in network modularity, we constructed a set of regression models focused on four factors that often influence female-female grooming relationships: (i) kinship (a binary predictor based on estimated, known, or imputed $r \geq 0.125$); (ii) rank similarity (i.e., 1 - the absolute difference in their proportional ranks); (iii) the recipient's relative rank (i.e., higher or lower); and (iv) shared male ties, defined as whether the pair of females held the same top male grooming partner in that year. Based on previous work in the papionins, we expected females to selectively groom their relatives and other similarly ranked group-mates (38–40, 48). Grooming also tends to be directed up the hierarchy (78), although this pattern is not ubiquitous (79). We expected these patterns to be diluted in species with female-biased dispersal (44, 45). In the multi-level societies, female-female relationships may be a byproduct of (or, in the case of hamadryas baboons, restricted by) shared male ties (51, 80). However, shared male effects could still subtly influence female relationships in the single-level papionins, in which ties to specific males might strengthen female-female relationships via shared proximity (e.g., olive baboons: 43, Kinda baboons: 53). To test these predictions, we constructed multi-membership models to assess the impact of these four factors on directed grooming patterns within each group-year (n = 133, excluding group-years with <4 females). For hamadryas baboons, we ran models focused solely on the impacts of rank metrics (randomized, as female hamadryas do not possess observable ranks, see *Materials and Methods)* and shared males, as kinship patterns are obscured by female transfer, and genetic sampling postdates the behavioral sample (44). We then extracted effect sizes and standard errors from these models and constructed a series of meta-analyses examining whether the magnitude of these effect sizes varied in response to the three social system categories, network size, and female dispersal patterns (i.e., female philopatric vs. female-biased dispersal).

Kinship was a robust predictor of female-female grooming relationship strengths across all three social structure types (**Figure 3a**). However, the strength of kinship effects varied across the sample. Kin biases tended to be stronger in larger grooming networks ($\beta_{GroupSize}$ = 0.55, 89% CI = [0.40, 0.70]), and the cliquish societies showed stronger kin biases than the cohesive societies (mean $\beta_{Cohesive}$ = 0.92, 89% CI = [0.54, 1.29], mean $\beta_{Cliquish}$ = 1.39, 89% CI = [0.90, 1.84]). Within the multi-level societies, kinship effects were considerably stronger in female-philopatric geladas than in female-dispersing Guinea baboons (mean $\beta_{Dispersal}$ = -1.84, 89% CI = [-2.82, -0.75]). Above and beyond the effects of kinship, rank similarity effects were moderate in the cohesive societies ($\beta_{Cohesive}$ = 0.21, 89% CI = [0.03, 0.39]), strongest in the cliquish societies (mean $\beta_{Cliquish}$ = 0.44, 89% CI = [0.22, 0.67]), and broadly absent in the multi-level societies (mean $\beta_{Multi\text{-}level}$ = -0.12, 89% CI = [-0.49, 0.25], **Figure 3b**). In the single-level societies, individuals also directed more grooming effort up than down the hierarchy, although this pattern was generally weak (mean $\beta_{Cohesive}$ = 0.32, 89% CI = [0.03, 0.62], mean $\beta_{Cliquish}$ = 0.23, 89% CI = [-0.12, 0.60). Sharing the same top male generally did not predict the strength of female-female grooming relationships in the cohesive and cliquish societies. However, this effect was very strong in the multi-level societies (mean $\beta_{Multi\text{-}level}$ = 2.23, 89% CI = [1.66, 2.79], **Figure 3c**), in which females residing in the same reproductive units typically shared the same top males.

Female-male grooming ties were variably shaped by social dominance

We then examined the effects of dominance rank on the strength of female-male grooming relationships, as female and male ranks broadly predict between-sex grooming interactions, which in turn often predict mating patterns (52, 54, 81). We constructed models for each group-year (n = 124, excluding group-years with <3 males) within the dataset to assess the relationship between directed female-male grooming interactions and: (i) male rank; (ii) female rank; (iii) the interaction between female and male rank; and (iv) the actor's sex. This interaction term allowed us to capture whether female-male relationships show rank assortment, which could reflect bidirectional competition for mating partners (i.e., high-ranking males could have priority of access to high-ranking females, and vice versa). Including the actor's sex as a predictor also allowed us to detect whether grooming was disproportionately directed by females towards males or was instead equitable within these dyads. In multi-level groups, males within the broader society do not show conventional dominance relationships (66, 82). For these societies, we labeled leader males as high-ranking (i.e., male rank = 1) and their follower males as low-ranking (male rank = 0). While these two male dominance metrics correspond with distinct social phenomena, they nevertheless reflect patterns of mating behavior and paternity success (40, 83–88). As above, we extracted the effect sizes for the predictor variables and then conducted meta-analytic regressions to determine whether the strength of these effects varied in relation to social system category and network size.

Across the sample, high-ranking and reproductively dominant males often received more grooming from females than low-ranking, subordinate males. However, these patterns were not universal. In particular, male rank effects were broadly weak and inconsistent across the single-level societies (mean $\beta_{Cohesive}$ = 0.23, 89% CI = [-0.03, 0.49]; mean $\beta_{Cliquish}$ = 0.20, 89% CI = [-0.11, 0.52]) but stronger in the multi-level societies (mean $\beta_{Multi\text{-}level}$ = 0.66, 89% CI = [0.34, 1.00], **Figure 3d**). Thus, male rank effects are often weak or absent in the single-level societies, in which males form linear dominance hierarchies, but consistent and widespread in the multi-level societies, in which males are either reproductively dominant 'leaders' or subordinate 'followers.' Across the papionins, female dominance rank had no consistent relationship with the strength of female-male grooming relationships (**Figure 3e**). Rank interaction effects were similarly weak across the papionins, and credible intervals for these effects overlapped zero for all three categories (**Figure 3f**). However, frequentist meta-analyses rather suggest that the cliquish societies show weak but detectable rank interaction effects (**Figure S2, Table S5**). In the single-level societies, females typically groomed males more than vice versa (mean $\beta_{Cohesive}$ = -1.36, 89% CI = [-2.15, -0.47]; mean $\beta_{Cliquish}$ = -1.33, 89% CI = [-2.31, -0.35]). However, grooming between the sexes was relatively equitable in the multi-level societies (mean $\beta_{Multi\text{-}level}$ = -0.78, 89% CI = [-1.80, 0.23]).

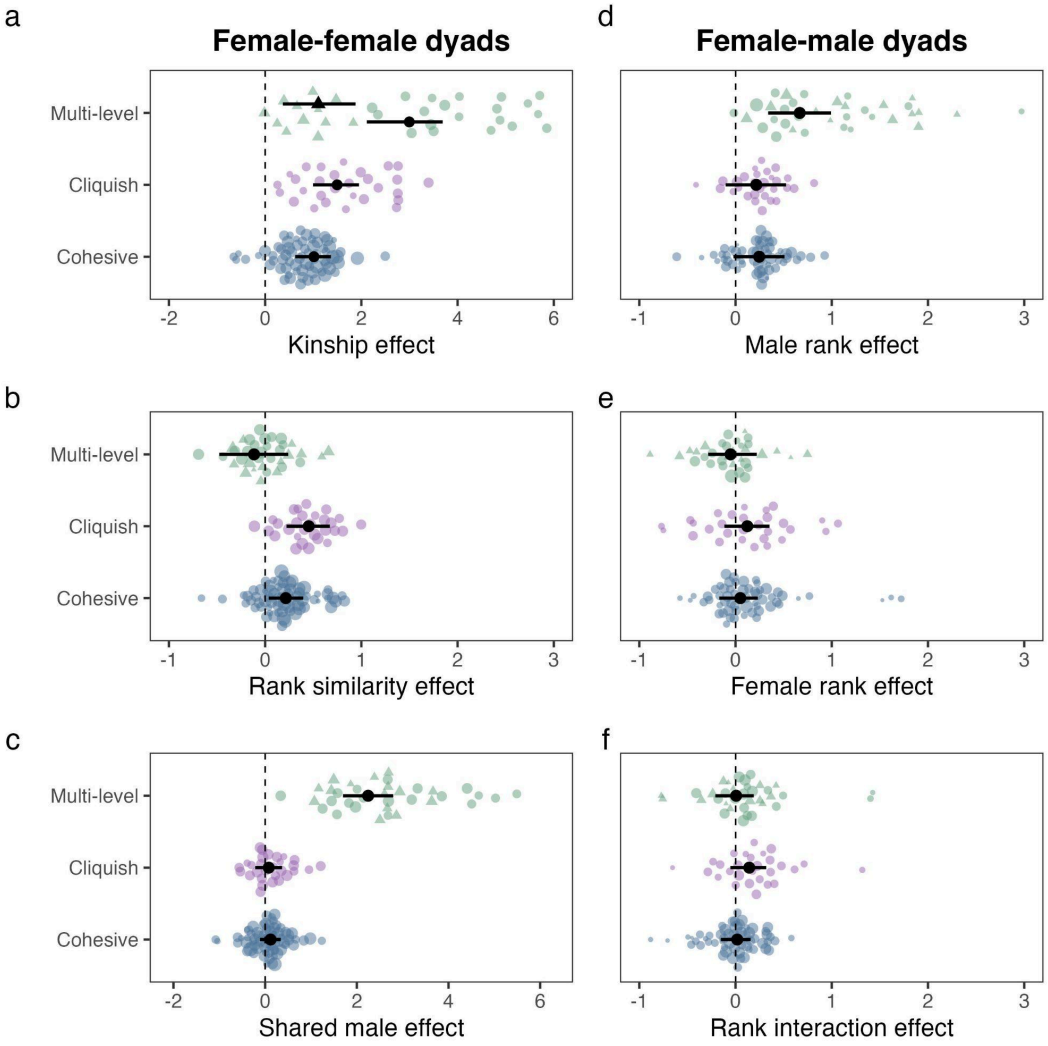

Figure 3. Social factors underpinning female-female and female-male grooming relationships. In (a,b,c) circles indicate species with female philopatry, and triangles indicate species with female-biased dispersal. (a). Kinship was a salient predictor of female-female grooming relationships, although this pattern varied across social systems and female dispersal patterns. (b) Rank similarity effects were generally positive, indicating that closely-ranked females groomed more often. However, these tendencies were strongest in cliquish societies and absent in multi-level societies. (c) Females that shared the same top male partners formed stronger grooming relationships in the multi-level groups but not in the single-level groups. (d) High-ranking and reproductively dominant males received more grooming from females, and this tendency was strongest in the multi-level societies. (e) High-ranking females did not typically form stronger between-sex relationships. (f) Rank interaction effects were likewise weak-to-absent across all three groups. Each point indicates a standardized effect size for the corresponding predictor. Black points and error bars indicate posterior means and 89% credible intervals. In (a) we provide a separate posterior estimate for species with female-biased dispersal, as this was the only case where dispersal patterns had a meaningful impact on the effect size of interest. The size of each point is scaled to 1 divided by the effect size's standard error. Thus, effects with greater precision are represented by larger points.

Nepotistic biases and shared male effects were independently linked with network structure

To determine whether the predictors of female-female and female-male grooming relationships underpinned interspecific variation in network structure, we constructed a set of models examining the influence of network size, social system type (single-level vs. multi-level, as this two-factor grouping showed more highly differentiated dyadic patterns, as described above), and the effects of kinship, dominance, and shared top males on network structure. These models were broadly similar to the network-level models described above but included additional predictors. The first set of models included the four effect sizes linked to female-female relationships (i.e., kinship, rank similarity, recipient's relative rank, and shared male effects), and the second set included the four effect sizes linked to female-male relationships (i.e., male rank, female rank, rank interaction, and grooming actor's sex). We propagated uncertainty throughout these models by including effect size standard errors as measurement error terms. For brevity, we focus on the drivers of network modularity, as this metric was more clearly differentiated across the three papionin social categories. However, models assessing the impact of these dyadic patterns on network density were qualitatively similar to those described below (**Figure S3, Table S5**).

Above and beyond the effects of social system type, the magnitude of female-female kinship ($\beta_{kinship.est}$ = 0.16, 89% CI = [0.03, 0.29]), rank similarity ($\beta_{rank.est}$ = 1.16, 89% CI = [0.74, 1.69]), and shared male biases ($\beta_{male.est}$ = 0.25, 89% CI = [0.12, 0.38]) all corresponded with increases in network modularity (**Figure 4**). By contrast, none of the effect sizes corresponding to female-male relationships were associated with network modularity. Taken together, these data indicate that increases in papionin network modularity primarily correspond with (i) stronger nepotistic and rank-related biases among females, which are elevated in the cliquish societies, and (ii) shared male ties among females, which are elevated only in the multi-level societies.

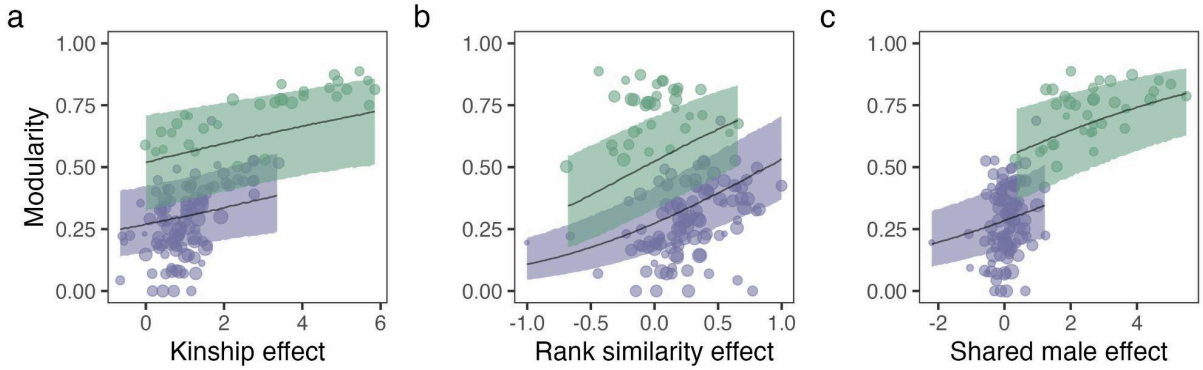

Figure 4. The predictors of female-female grooming patterns were linked with the extent of group-level modularity. Stronger effect sizes for (a) kinship, (b) rank similarity, and (c) shared male effects were all associated with greater network modularity. Blue points and bands indicate network measures and 89% credible intervals for the single-level societies, while green points and bands indicate network measures and 89% credible intervals for the multi-level societies.

DISCUSSION

Using a new, rich comparative dataset, we captured wide variation in group structure and its underpinnings across the papionins. As expected, species that live in single-level societies formed groups that were denser and less modular than species that live in multi-level societies. However, the single-level species were structurally diverse and could be divided into two distinct categories. Mandrills, Kinda baboons, and chacma baboons ('cliquish' societies) formed grooming networks that were consistently more modular than those of yellow baboons, olive baboons, Sanje mangabeys, sooty mangabeys, and gray-cheeked mangabeys ('cohesive' societies). Both supervised and randomized approaches provided empirical support for this categorization scheme, suggesting true biological differences. The three social structure categories mapped onto variation in the social

factors that shaped the strength of female-female grooming relationships. Although kin and rank biases were often salient and taxonomically widespread, these tendencies were elevated in the cliquish societies. Shared male ties played a central role in only the multi-level species. In turn, these nepotistic biases and shared male effects were independently linked to increases in network modularity. While female-male grooming relationships were strong in many papionin groups, the rank-structuring of these ties did not predict variation in network topology. Below, we discuss how these social strategies may be tailored to distinct social and ecological pressures and propose comparative tests that might further uncover the proximate and ultimate drivers of this variation.

What generates variation in social structure among the single-level societies?

While network size was generally higher in the cliquish species than in the cohesive species, differences between their social networks persisted even after accounting for group size. These patterns could in part be a byproduct of papionins' evolutionary history. For example, chacma baboons and Kinda baboons, which both form cliquish groups, are closely related and share a history of extensive admixture (70, 89–91). However, phylogenetic similarity cannot explain the evolution of the cliquish social structure observed in distantly related mandrills, suggesting an additional role of social or ecological pressures in generating convergence across these taxa. For instance, harsh or highly seasonal environments could generate increased female-female competition over food resources, thereby encouraging females to prune their social ties (92, 93) and forcing males to divide their time between spatially distinct female subgroups (62). Forthcoming analyses using the CAPS database will aim to test this ecological hypothesis by linking variation in social network structure with key measures of environmental productivity and seasonality. However, not all cliquish species occupy particularly harsh or seasonal environments (94, 95), and papionin groups do not always become more fragmented during resource-poor conditions (96–98).

Instead, the heightened modularity we observed in cliquish groups could reflect competition over male partners. Males within the cliquish societies tended to attract more grooming than males in the cohesive societies, although males groomed females back at much lower rates (except in Kinda baboons: **Figure S1**). It is notable that all three cliquish taxa show marked – if contrasting – signatures of sexual selection. Both chacma baboons and mandrills exhibit high canine and body size dimorphism (99), and male mandrills further display conspicuous facial coloration (100). These characteristics correspond with heightened contest competition over mating opportunities (101, 102), high levels of male reproductive skew (40, 84, 103), and, perhaps, elevated infanticide risk (95, 104), which could incentivize females to form relationships with likely sires to protect their vulnerable offspring (54, 105). By contrast, Kinda baboons have high relative testes sizes and exhibit mating patterns that are more indicative of indirect forms of male-male competition (106, 107). Thus, strong female-male relationships in Kinda baboons are more likely a product of mate choice and may serve a different adaptive function (e.g., offspring developmental benefits: 108). In both of these systems, limited male attention could exacerbate female-female competition, thereby heightening female social selectivity. More broadly, the drivers and consequences of between-sex bonds are highly variable across primates and other mammals (reviewed in 15). Future analyses using the CAPS datasets will target more subtle differences in the exclusivity, equitability, and durability of between-sex bonds across the papionins.

Kinship and rank variably predicted strength of grooming relationships

As expected, maternal kinship was a robust predictor of grooming relationships across the papionin species. Kinship effects were strongest in geladas, moderately strong in the cliquish societies, weaker in the cohesive societies, and weakest in Guinea baboons, in which females disperse from their natal units. In sum, the papionins appear to vary in the extent to which females bias their efforts towards kin (see also 43), and these patterns may reflect the relative availability of close kin, the overall shape of the competitive landscape, and the resulting strength of kin selection. If so, then the stronger kinship effects observed in the cliquish societies could reflect a harsher competitive landscape, and these forces may become stronger at large group sizes. Kinship effects tended to be

stronger in larger groups across the papionins, perhaps because mean relatedness declines and variance in relatedness increases as groups become larger (109). Across mammals, social groups tend to become more differentiated when close relatives are scarce and mean relatedness is low (110). However, it remains unclear whether differences in mean relatedness explain wholesale differences in network-level structure both within (e.g., hyenas: 111, but see macaques: 112) and across taxa (e.g., bats: 113). Further genetic sampling and modeling approaches (e.g., 114) will be necessary to quantify these kinship patterns and determine whether group demography mediates the relationship between group size and social structure.

Dominance rank effects were similarly widespread but highly variable. In general, female-female dyads that were close in rank tended to groom more than dyads that were further apart in rank. While kin also tend to be closer in rank (due to maternal rank inheritance: 47, 115, 116), these rank similarity effects persisted even after accounting for kinship. Indeed, prior studies on papionin groups suggest that rank similarity is most tightly linked with the strength of non-kin relationships (38, 39, but see 48). In general, rank similarity effects were weaker in the cohesive societies than in the cliquish societies, which may be marked by more intense forms of female-female competition. Previous research suggests that cohesive baboon females compete mainly over food resources (60, 117), while cliquish baboon females compete more explicitly over male partners (54, 105). If male attention is less easily shareable than food, as noted above, this could help explain these stronger rank effects. Rank effects were generally absent in the multi-level societies, perhaps because competition over both foods and males is broadly reduced both within and between their one-male units (96, 97, 118). Indeed, in hamadryas baboons, dominance ranks do not appear to even exist (51). More targeted analyses are needed to determine if and how the strength of competition over food and mates differentially shapes the tenor of female-female relationships.

Rank effects on female-male relationships were similarly variable. High-ranking, dominant males tended to receive more grooming than low-ranking subordinate males, although this pattern was only salient in the multi-level societies. This difference may be in part a reflection of our choice of social dominance measures for the single- (i.e., proportional rank) and multi-level societies (i.e., leader vs. follower). In other words, the magnitude of male rank effects may vary as a function of males' social and reproductive control (15, 56). In multi-level societies, leader males can monopolize access to the females within their units (49, 50, 119). By contrast, in single-level societies, low- and mid-ranking males can more frequently secure reproductive opportunities (120), often by forming strong grooming relationships and consortships with particular females (85). Female rank had little effect on female-male grooming, suggesting that papionin females do not systematically compete for access to males. Rank interaction effects (which could reflect assortative mating patterns: 81, 121) were similarly rare across the sample. However, there were some group-years where these effects were present, particularly within the cliquish taxa. Thus, females might still compete for access to high-ranking males in some contexts, such as when they have sired their current offspring and can provide anti-infanticide protection (54, 105). In combination, these data suggest that dominance rank effects are highly variable, likely because females compete over different resources (e.g., access to food vs. protective males: 117, 118, 122) and males face varying degrees of mate competition (as indexed by reproductive skew: 40, 83–87).

Shared male effects were limited to the multi-level societies

As in previous research on these study populations, we found that females in multi-level societies primarily groomed females from their own reproductive units (48, 49, 51), generating strong shared male effects. These patterns were pronounced across all three multi-level taxa, despite variation in the observed degree of female social agency. In particular, female Guinea baboons can move freely between units (49), female geladas are incentivized to focus solely on the close kin within their units (47), and female hamadryas are largely restricted by their leader males (67). In some single-level societies, females who share the same preferred males form stronger spatial associations (43), generating conditions that could circumstantially strengthen their grooming relationships. We

expected this pattern to emerge in species like olive and Kinda baboons, in which unrelated females often share the same top male partners across multiple birth seasons (52, 53). However, shared male effects were negligible across the single-level papionins. In other words, shared male preferences might bring females into close proximity without prompting the formation of close grooming relationships, perhaps because these overlapping females instead compete over access to their shared male. In this way, the between-sex bonds documented in the single-level societies (52, 54, 105, 123) are likely distinct from those found in the multi-level societies (49–51), as the latter are more integral to grooming network structure (124).

In combination, these patterns suggest that the processes that enhance modularity within the single-level societies (i.e., kin- and rank-related grooming biases) differ from the processes that generate extreme modularity within the multi-level societies (i.e., shared male patterns). In other words, the cliquish papionins likely do not recapitulate the evolutionary transition from a single- to a multi-level society. However, none of the chacma baboon groups included here formed one-male units during these study periods (62). Likewise, recent research has identified more subtle similarities between single-level Kinda baboons and multi-level Guinea baboons, as their between-sex bonds are relatively bidirectional, enduring, and largely shaped by female mate choice (49, 53). Thus, our dataset may not capture all the contexts in which single-level societies can resemble multi-level societies. Because chacma and Kinda baboons have both been positioned as basal members of *Papio* in genomic analyses (34, 89), it remains possible that ancestral baboons formed cliquish groups and were thus predisposed to evolving more modular social structures. However, the putative ancestral condition for geladas is more ambiguous. While ancestral *Theropithecus* may have been cliquish like the presumed ancestor of *Papio,* it could instead have mirrored the small, cohesive groups of *Lophocebus* (i.e., the gray-cheeked mangabeys). If so, then small, mangabey-like ancestral groups could have coalesced into the large supergroups observed in extant geladas (more closely mirroring the evolutionary pattern inferred for multi-level Asian colobines: 125). These differing evolutionary pathways underscore the fact that – despite their structural commonalities – multi-level societies are diverse in their overall shape, presumed functions, and evolutionary histories.

CONCLUSIONS

This new dataset provides a systematic foundation for mapping behavioral variation across the papionins and identifying the social processes that produce between-species differences in social structure. Taken together, our analyses demonstrate that the papionins are more socially diverse than has been historically recognized. Beyond the well-known distinction between species that form single-level and multi-level societies, our analyses show that single-level societies can be further divided into two social categories, cohesive and cliquish. Kin biases consistently influenced females' grooming behavior across the papionins, but female-female rank biases were markedly elevated in cliquish societies and shared male patterns were only pronounced in the multi-level species. It remains unclear, however, why natural selection has favored these particular strategies. Further analyses using the CAPS database – in combination with ongoing efforts to trace papionins' genomic histories and uncover signatures of ancient selection (34, 89, 126–128) – may provide novel, complementary insights into the evolution of sociality.

MATERIALS AND METHODS

Study sites and populations

The data used for this study were collected across several wild populations of African papionins (see **Table S1** for a list of projects contributing to CAPS). Details regarding the demographic histories and data collection methods across these long-term research projects can be found in previous reports (40, 41, 48, 52, 67, 88, 106, 122, 129–134). Each contributing study provided the records necessary to construct most or all of the following data frames: (i) study subjects; (ii) group membership; (iii) behavioral observations; (iv) grooming interactions; (v) dyadic kinship; (vi) female and male ranks, aggregated as yearly mean. Below, we describe how these datasets were constructed, how this information varied across sites, and how we treated missing information.

Study subjects and group membership

Contributing projects provided either (i) known and/or estimated dates of birth or (ii) age category transition dates (e.g., subadult to young adult, etc.) for all adult female and male subjects that were included in behavioral sampling. In total, the sample comprised 1146 unique subadult and adult individuals (684 females, 462 males) residing within 28 distinct social groups (1-5 groups per population, **Table S1**). When constructing social networks, we included females if their known or estimated age was ≥ 4 years or if they were classified as subadults/adults during that calendar year. This age approximates the onset of sexual maturity in females from many papionin populations (135–138). Likewise, we included males if their known or estimated age was ≥ 7 years or if they were classified as subadults/adults during that year. This age roughly follows the onset of secondary sexual characteristics, the timing of natal dispersal events, and the attainment of dominance in males in many of these study populations (137, 139–141). To determine periods of co-residence among each pair of individuals, we used group membership data from each study site, which noted when individuals 'entered' (due to their birth, the study's onset, or their immigration) or 'exited' (due to their death, disappearance, or dispersal) their respective social groups. This allowed us to exclude behavioral samples collected when pairs were no longer co-resident when calculating dyadic observation effort. Most individuals belonged to one social group throughout the study periods. However, males (n=47) occasionally dispersed from one study group into another, and females (n=10) occasionally switched social groups via dispersal (in Guinea baboons) or during group fission events (in the olive baboons at Laikipia).

Behavioral observations and grooming interactions

Each contributing study site provided records of behavioral observation at the individual-level. In most cases, behavioral data were collected via continuous focal animal samples, during which the direction and duration of the focal animal's grooming interactions were recorded. However, at some study sites (Amboseli and Gashaka, **Table S1**), grooming events were collected opportunistically while researchers moved about the study group and collected other routine data (e.g., focal samples). This method of data collection, termed representative interaction sampling, and associated procedures used to correct for sampling densities at the group-level have been described elsewhere (68, 142). In short, because grooming observations extended beyond the focal individual, observation effort was calculated not at the individual-level but at the group-level (i.e., mean number of focal samples per female). For one population (Filoha), social interactions were recorded during unit-level scans collected at ~10-minute intervals (51).

Kinship estimates

Kinship was determined using a mixture of maternal pedigree information (available from all sites to varying depths), genetically confirmed paternities (Simiens: 143, Amboseli: 144), and genetic relatedness estimates (Simenti: 145). Using this information, we calculated the relatedness of all dyadic pairs and then designated dyads as being related if estimated $r \geq 0.125$. Given differences in pedigree depth and genetic sampling coverage, sites varied widely in the relative representation of related, unrelated, and unknown dyad pairs. Thus, to avoid potential biases (i.e., mother-offspring dyads may be more readily discernible than sisters during short-lived studies, thereby inflating

maternal kinship effects on grooming) and to ensure the inclusion of all study populations, we implemented imputation procedures to categorize unknown dyads using informative criteria (see *Supporting information* for more details). However, we did impute kinship data for hamadryas baboons, as these data were limited. When conducting analyses focused on female-male dyads, we removed related pairs, as kin dyads are unlikely to form mating relationships (e.g., 146).

Dominance ranks

Data on dominance rank were (i) directly provided by the collaborating research projects or (ii) calculated from directed agonistic interactions using the 'EloRating' package (147). To standardize dominance ranks within each study group, we calculated rank as the proportion of all same-sex group members that each individual outranked. However, given differences in the scale of competition across the multi-level societies, we calculated ranks differently in these three species. Specifically, female ranks in geladas were calculated at the level of the reproductive unit (47), as between-unit aggression is quite rare and competition is highly localized, while female ranks in Guinea baboons were calculated at the party-level (148). By contrast, wild female hamadryas baboons rarely engage in aggression, so dominance ranks were inestimable (51). Thus, we treated dominance effects in hamadryas baboons in two ways: (i) by imputing random dominance ranks for each female to recover a presumed null effect or (ii) by fixing dominance rank effects to 0 for this species, which produced comparable model outputs. Likewise, males in multi-level societies do not form clear dominance hierarchies across their entire 'bands' or 'parties.' Thus, we categorized leader males as having ranks of 1, and follower males as having ranks of 0.

Social network construction

Annual group-level social networks were constructed and visualized in 'igraph' (149) using matrices corresponding to (i) dyadic observation effort, measured in minutes for continuous focal observations, as the number of scans for one-male unit scan data, or per capita observation effort for 'representative sampling' (68), and (ii) the total duration of grooming bouts or the count of grooming events or scans, depending on how grooming observations were recorded. This allowed us to calculate edge weights that accounted for differences in observation effort. From these social networks, we calculated (i) density, which captures the proportion of dyads that were observed grooming; and (ii) modularity, which captures the tendency for individuals to groom within vs. between subgroups (i.e., 'communities') that were assigned via random walks.

Statistical analyses

First, to model the impacts of social structure type and network size on density and modularity, we constructed a series of models in 'brms' (71). Our fixed effects included network size (i.e., the number of adults and subadults in the network), observation effort per capita, and social structure categories. We initially included interaction terms to identify differences in network scaling across our social system categories. However, these did not improve model fits. To account for phylogenetic history, we estimated a random effect constrained by a phylogenetic covariance matrix in these models, using the primate phylogeny provided in (70). If sampled species were not present in the phylogeny (as was the case for the three mangabey taxa), we used closely related congeners that match their relative phylogenetic position. We also included species, population, and social group identities as nested random effects. This approach allowed us to account for variation in network structure that was attributable to (i) phylogenetic history and (ii) species-specific traits that are independent of their phylogenetic history. To assess differences in the predictive power of our two categorization methods (i.e., single-level or multi-level, vs. cohesive, cliquish, and multi-level), we constructed the following models for both network-level metrics: (i) a two-level predictor model, (ii) a three-level predictor model; and (iii) a network size only model. For density, including social category as a three-level predictor did not provide significant improvement over the two-level predictor. However, for modularity, the three-level model substantially outperformed the two-level model. Thus, we reported the results from this three-level model in the Main Text and treated these categories as biologically relevant in all subsequent analyses.

Second, to determine the factors that underpin social relationships across populations, we constructed a series of dyadic regression models in 'brms.' For each group-year in the dataset (n = 133, excluding group-years with <4 adult or subadult females), we constructed a zero-inflated negative binomial model, where directed dyadic grooming (in events, scans, or the rounded number of minutes; two directed observations for each dyad-year) was treated as an integer outcome. In each of these models, we included kinship ($r \geq 0.125$, yes/no), rank similarity (measured as 1 - the dyad's absolute proportional rank difference), the partner's relative rank (higher or lower), and shared top male (yes/no) as fixed effects, and included observation effort as a logged offset term. When rank data were missing (because she had yet to enter the dominance hierarchy, because her Elo-rating had yet to stabilize, etc.), we included her rank from the first year she was included in the dataset. We included actor and recipient identities as multi-membership random effects to account for interdependence. As noted above, dyadic covariates were missing for some female-female dyads. Thus, we used classification and regression tree imputation procedures using the 'mice' package (150) to fill in these missing data. Specifically, we imputed individual attributes (proportional ranks) and dyadic covariates (kinship) based on informative criteria. Critically, the imputation of these missing data did not systematically bias our effect size estimates (see *Supporting information*). For each group-year, we pooled model estimates across five imputed datasets using the brm_multiple function in 'brms' (71)

We used a similar process when modeling the predictors of female-male relationship strengths, using female proportional rank, male proportional rank, their interaction, and the grooming actor's sex as fixed effects. For each group-year in the dataset (n = 124, excluding group-years with <3 adult or subadult males), we constructed a zero-inflated negative binomial model, where dyadic grooming (in events or scans or the number of minutes) was treated as an integer outcome variable. We included logged observation effort as an offset term, and actor and recipient as multimembership random effects. This inclusion allowed us to detect rank- and sex-related biases in the distribution and direction of grooming within and across female-male dyads. We again included randomized ranks for hamadryas baboon females, given their lack of clear dominance ranks in the wild (51). As above, we used imputation procedures to include males with missing rank information and pooled model estimates across five imputed datasets for each group-year. We then extracted effect size estimates and standard errors to use in subsequent meta-analyses.

We then constructed a series of eight phylogenetic meta-analyses in 'brms' to model the drivers of the dyadic effects listed above (female-female dyads: kinship, rank similarity, the recipient's relative rank, and shared male effects; female-male dyads: female rank, male rank, their interaction, and actor sex). Each effect size was treated as a student-distributed outcome, as this better handled outliers within the data. In these models, we incorporated the effect size's standard errors to account for measurement uncertainty. We included social categories (cohesive, cliquish, multi-level), network size, and female philopatry (yes/no, female-female effects only) as fixed effects in each of these models. We also controlled for phylogeny, species, population, group identity, and group-year using random effects. This allowed us to extract observation-level (i.e., residual) variance when calculating intraclass correlation coefficients (**Figure S4**). To assess the robustness of these results (151), we also performed more traditional, frequentist meta-analyses using 'metafor' (152). The output of these models was largely concordant with the Bayesian approach.

Lastly, we ran additional models to determine whether these dyadic effects indeed contributed to group structure. These analyses mirrored the overall structure of the primary models assessing the influence of network size and social system on network metrics described above. Here, however, we included the effect sizes listed above as additional covariates and accounted for measurement uncertainty by using their respective standard errors. In this analysis, we used the two-factor social categories in order to determine whether increases in the magnitude of kin and rank biases underpin the differences between the cohesive and cliquish taxa. As above, we controlled for phylogenetic relationships, species, population, and group identities by using nested random effects. Across all

models, we used weakly informative prior distributions and followed previous recommendations when constructing Bayesian meta-analyses (151). We ran each model for 4 chains with 4000 iterations (1000 warmup), assessed model fits using posterior predictive checks, and provided 89% credible intervals throughout the Main Text. To reduce the number of divergent transitions, we set 'adapt_delta' at 0.99 and 'max_treedepth' at 15 for all models. Effective sample sizes were sufficiently large (>1000), R-hat values were ~1, and chains were convergent across all models.

DATA AVAILABILITY

The data and code necessary to reproduce these analyses and associated visualizations are available on GitHub (https://github.com/PapioninSocieties/Feder_et_al_CAPS_2025) and have been archived on Zenodo (https://doi.org/10.5281/zenodo.16422722).

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