

Individual differences in coping styles and associations with social structure in
wild baboons (*Papio anubis*)

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The patterning of interactions between individuals over time form the foundation for relationships, which are the basis for social group structure. The emergent social structure scaling from interactions might, therefore, be influenced by individual differences in how individuals respond to stressors and uncertainty, which are often intrinsic aspects of social dynamics. During a 17-month study of wild olive baboons, *Papio anubis*, in Laikipia, Kenya, we measured individual differences in coping style and stress reactivity by experimentally presenting a stressor with multiple solutions. We measured individual differences in sociality through focal animal and ad libitum sampling that recorded grooming, aggression, proximity, and social displacements. We examined whether experimental measures of coping style and stress reactivity (1) are linked to social network assortativity, (2) predict network position and (3) covary with social dominance rank. Homophily was observed for coping styles in a strong proximity network but not when weak associations were included in the analysis. Coping style scores did not predict social network strength or degree. Partner stability indices of proximity associations and social dominance rank did not covary with coping style measures. Static summative network structures may obfuscate investigative inquiries into the role of individual differences and, also, may constrain or facilitate the behavioural expression of such differences. Thus, we should prioritize more fine-grain investigative approaches inclusive of variation in situation, context and consistency of group structure.

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social responsiveness

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There are numerous frameworks for quantifying individual differences that are consistent over time, such as personality, temperament and coping styles (Réale et al., 2007). Consistent individual differences can additionally be quantified using multiple methods; for instance, rating or coding of natural behaviours, responses to experimental paradigms or cumulative observer experience (Freeman & Gosling, 2010). These diverse frameworks and methods have isolated numerous personality-like traits in nonhumans. We focus on individual differences in the stress response system, quantified and interpreted under the coping style and stress reactivity framework, often using experimental paradigms (Koolhaas et al., 1999; Steimer et al., 1997). Within this framework, individuals are quantified on two orthogonal continua based on how they respond to a stressor (coping style) and the magnitude of their response (stress reactivity). Coping styles are viewed on the proactive–reactive continuum: a proactive coping style facilitates ‘rapid’ impulsive and aggressive responses that function to exert control over a stressor and are more predictable in a social context relative to reactive individuals, which are more behaviourally flexible and show greater inhibition in response to a stressor (Coppens et al., 2010). For instance, when laboratory rats, *Rattus norvegicus*, are experimentally confronted with an electric probe, more proactive individuals are likely to exhibit confrontational burying behaviour, while more reactive individuals tend to engage in freezing behaviour (Koolhaas et al., 1999). Stress reactivity quantifies the severity of the response to the stressor, often measured through the expression of fear- and anxiety-associated behaviours.

Coping style variation has been implicated to influence social outcomes because of its covariance with social responsiveness: an individual’s ability to incorporate information from conspecific behaviour into its own decision making (Aplin et al., 2013; Coppens et al., 2010; Snijders et al., 2014; van Oers et al., 2005; Wolf et al., 2011). For example, more reactive male great tits, *Parus major*, resumed feeding faster post-startle when paired with active companions, while more proactive males did not change behaviour based on companion activity (van Oers et al., 2005). Coping styles are a proposed outcome of an evolved speed–accuracy trade-off to facilitate distinct solutions for contextually distinct stressors (Coppens et al., 2010; Wolf & Weissing, 2010). Relative to reactive individuals, the proactive coping style is associated with more rapid, more patterned, less behaviourally flexible responses, which result in

higher predictability in a social context (Coppens et al., 2010; Wolf et al., 2011), whereas more socially responsive reactive individuals gain greater benefits from increased environmental sampling (Wolf et al., 2008, 2011). The current lack of comparative data on individual covariation in the stress response system and in social life, however, seriously limits interpretations of primate social evolution.

How individuals respond to stress and associated differences in social responsiveness, therefore, is of importance in a complex social system. Social life can itself induce stress via the unpredictable or uncontrollable nature of interactions (Koolhaas et al., 2017; Sapolsky, 2004). Iterative interactions, however, may create long-term relationships vital to reducing social stress (Kummer, 1978; Silk et al., 2013). Hinde (1976) and Kummer (1978) emphasized the possible importance of intrinsic individual differences to social relationships, but little is presently known regarding how individual differences relate to position within prosocial (Krause et al., 2010) and agonistic networks, as well as social dominance hierarchies, despite a growing body of literature linking the stress response system with social connectivity (Kornienko et al., 2020; Mercado & Hibel, 2017).

Here we consider whether fundamental individual differences in the stress response system cascade into agonistic and prosocial interactions; do such differences influence the social position of a wild primate? In this study, we integrate field experiments and behavioural observations on wild olive baboons, *Papio anubis*, to study how individual differences in the stress response system interact with sociality in a natural setting characterized by uncertainty and social complexity. We collected experimental measures of coping style and stress reactivity and long-term focal data for social networks and hierarchies. We explored whether gross group level differences in individuals' associations (assortativity) are attributable to coping style and stress reactivity variation. We examined whether differences in the quality and quantity of associations covary with coping styles. Finally, we examined whether social dominance rank (rank) covaries with coping style.

Group assortment can manifest along a continuum from homophilic to heterophilic. If individuals associate more readily with conspecifics that share a similar phenotypic trait, then such networks exhibit high homophily (Lazarsfeld & Merton, 1954; McPherson et al., 2001; Rivera et al., 2010), while networks defined by dissimilar associations exhibit high heterophily (Lazarsfeld & Merton, 1954; Lozares et al., 2014; Rivera et al., 2010). In human social networks, homophily tends to be the predominant pattern of assortment (McPherson et al., 2001). Similar observations have been made for homophily in boldness and sociability-like personality traits for captive chimpanzees, *Pan troglodytes* (Massen & Koski, 2014), and wild Assamese macaques, *Macaca assamensis* (Ebenau et al., 2019). Homophily along coping styles has been demonstrated using measures of exploratory behaviour, often used as a measure of coping style in great tits (Carere et al., 2001; Koolhaas et al., 1999). Males with similar exploratory scores were more likely to proximally associate at feeder platforms (Aplin et al., 2013) and maintain neighbouring nests (Johnson et al., 2017). The relationship between assortativity and personality traits, however, may be more complex than indicated by these studies. For instance, Carter et al. (2015) broadly observed patterns of homophily with boldness in the grooming networks of chacma baboons, *Papio ursinus*, but these patterns fluctuated in strength across study groups and years.

Social Network Position

Several studies, predominantly in rodents and birds, have provided insight into the influence of coping style variation on social interactions and, as a consequence, individual position within a social group. More proactive rats consistently utilize aggression as a response to a stressor (Coppens et al., 2010; Koolhaas et al., 1999), facilitating social predictability but potentially impeding prosocial interactions. Thus, individuals with a proactive coping style benefit from a greater number of weaker social bonds characterized by frequent acts of aggression, relative to reactive conspecifics. Social responsiveness and behavioural flexibility, instead, limits predictability (Wolf & Krause, 2014). Thus,

individuals with a more reactive style functionally benefit from fewer social bonds of greater strength and cohesion relative to proactive individuals. In wild great tits and house finches, *Haemorhous mexicanus*, proactive coping individuals exhibited higher degree, eigenvector and betweenness network centrality measures (Aplin et al., 2013; Moyers et al., 2018; Snijders et al., 2014), while reactive great tits had stronger associations (Aplin et al., 2013). In common degu, *Octodon degus*, however, Chock et al. (2017) found no associations between social position and exploratory or boldness personality traits, potentially due to a focus on associations in burrows that may reflect parental care behaviour.

Here we examined several broad social networks: affiliative grooming, proximate associations and aggressive interactions. In baboons, grooming is a common measure of relationship quality (Silk et al., 2013) and may be used to increase tolerance (Sick et al., 2014). Proximity introduces a more varied element of relationships; all else being equal, the probability of positive or negative interactions increases with proximity (Farine, 2015). Baboon proximity networks have been positively associated with prosocial networks (King et al., 2011), but this association varies across years and groups (Castles et al., 2014). Aggressive social tendencies are a core element of the coping style framework (de Boer et al., 2003; Koolhaas et al., 1999) and are incorporated here as social network measures to facilitate greater resolution of the group structure regarding aggression, rather than previous approaches using individual rates (Pritchard & Palombit, 2022a). Research on baboons has enhanced our understanding of the role that individual differences play in the patterning of their social lives. For instance, boldness in chacma baboons influences patterns of co-association (Carter et al., 2015) and social decisions during foraging (Carter et al., 2013). This research expands upon this investigative approach.

Social Dominance Hierarchies

While social dominance is partly an emergent social property of the group, rank is potentially influenced by individual differences (Chase et al., 2002; Sapolsky, 2005). In male baboons, coping style is expected to show a relationship with rank because social status is partially attained through agonistic

social interactions (Strum, 1982).

Literature examining coping styles in the context of social dominance rank reveal contradictory findings about whether reactive or proactive individuals are more adept at securing higher ranks. For instance, more reactive great tits had higher average dominance ranks in long-term group housing conditions (Verbeek et al., 1999), but proactive individuals were more likely to initiate and win brief experimental pairwise contests (Verbeek et al., 1996). Such contrasting outcomes might reflect the consequence of different selection pressures in the wild (Verbeek et al., 1999), with coping style differences providing contextually specific benefits. The reactive coping style is defined by an increased capacity to adjust behaviour to a stressful situation via behavioural flexibility, while proactive coping style responses exert control over stressful circumstances (Coppens et al., 2010; Verbeek et al., 1999). Thus, long-term associations might favour high rank in reactive coping individuals. Interestingly, rhesus macaques, *Macaca mulatta*, with more aggressive personality types disperse earlier (Cote et al., 2010; Higley et al., 1992; Taub & Vickers, 1994), lending support for the possibility that a proactive coping style confers a greater advantage during uncertain and costly dispersals (Alberts & Altmann, 1995), while a reactive coping style could be more advantageous during group residency.

Alternatively, increased inhibition in decision making during stressful interactions for reactive individuals may be costly during agonistic contests, impeding their capacity to secure rank rapidly. In mice (*Mus musculus*), individuals with more proactive coping styles showed greater success in controlling territories under stable group conditions with high population density (van Oortmerssen & Busser, 1989) and secured higher social dominance within their colonies (Blanchard et al., 1988), relative to reactive individuals. In Barbary macaques, *Macaca sylvanus*, and vervets, *Chlorocebus aethiops sabaenus*, behaviourally measured high-ranking individuals scored higher on survey-rated factors with confidence and assertive personality items, relative to low-ranking individuals (Konečná et al., 2012; McGuire et al., 1994).

Although specific evidence for the influence of coping styles on rank attainment does not exist in baboons, individual 'behavioural styles' was not correlated with rank in olive baboons (Ray & Sapolsky,

1992; Sapolsky, 1994; Sapolsky & Ray, 1989; Virgin & Sapolsky, 1997) and boldness was not correlated with rank in chacmas (Carter et al., 2015). Covariation of coping style with social dominance rank, however, cannot yet be excluded with confidence because rank was previously high–low dichotomized across studies (Ray & Sapolsky, 1992; Sapolsky & Ray, 1989; Virgin & Sapolsky, 1997), making delineation of more subtle effects difficult to measure. Additionally, boldness may or may not equate to coping style (Blaszczyk, 2017; Bolig et al., 1992; Finkemeier et al., 2018; Koolhaas et al., 2007; Pritchard & Palombit, 2022b).

Hypotheses

Hypothesis 1

We examined whether coping style and stress reactivity variation correspond to group assortativity (Newman, 2002; Carter et al., 2015). Analyses on the covariance of assortativity with coping style and stress reactivity were lacking, but we drew upon similar approaches examining assortativity and boldness. Boldness has been posited as relevant to coping style or stress reactivity (Blaszczyk, 2017; Bolig et al., 1992; Finkemeier et al., 2018; Koolhaas et al., 2007; but see Pritchard & Palombit, 2022b). The findings of Carter et al. (2015) suggested that homophily is observed in prosocial networks along axes of coping style and stress reactivity (Prediction 1).

<H3>Hypothesis 2

We next examined whether individual coping style influences the number and strength of social bonds (Wolf & Krause, 2014). As assortativity measures do not permit multivariate analyses using weighted networks (Carter et al., 2015), other metrics may be used to gain insight into social position. We predicted that individual baboons exhibiting a more proactive coping style would groom more partners (Prediction 2a), maintain close proximity to more partners (Prediction 2b) and aggress at higher rates to relatively more partners (Prediction 2c). We also predicted that individuals exhibiting a more reactive

coping style would spend more time associating with the same conspecifics (Prediction 2d).

<H3>*Hypothesis 3*

Finally, we examined whether individuals' consistency in response to a stressor is associated with their social rank attained as an outcome of agonistic interactions. Assuming a stable hierarchy, we predicted that males with a reactive coping style would have higher rank relative to more proactive males (Prediction 3a). Alternatively, we predicted that males with a proactive coping style would have higher rank than more reactive males (Prediction 3b). We acknowledged the possibility that neither Prediction 3a nor Prediction 3b would be supported; instead, coping style may not covary with rank (Moyers et al., 2018). Support of the null hypothesis would be theoretically important given prior emphasis on context-specific trade-offs for coping style variation (Dingemanse & Goede, 2004; Koolhaas et al., 2017; Korte et al., 2005; Verbeek et al., 1999).

METHODS

Study Subjects and Field Site

Fieldwork took place between November 2017 and April 2019 during R.A.P.'s ongoing long-term 'Project *Papio*' (Lynch et al., 2020) in Laikipia, Kenya (0°15'29"N, 36°44'49"E). A.J.P. studied 44 adult male and female subjects in two habituated groups of olive baboons, Kati-Kati and Shire. Kati-Kati had 90 individuals, with 9 adult females and 19 adult males; an additional eight females started cycling and five of those individuals bore offspring during the study period. Shire had 33 individuals, with 8 adult females and 8 adult males; an additional four females started cycling and one of those individuals became pregnant during the study period. Only adults were studied, as individual differences exhibit growth trajectories until adulthood (Clarke & Boinski, 1995; Suomi et al., 1996).

The field site is primarily *Vachellia (Acacia) drepanolobium* shrubland savannah. The baboons ranged over five ranch and community properties with mixed land use comprising primarily Samburu

pastoralism, cattle ranching and tourism. Both groups used five sleep site locations, which they often shared, and they ranged together during the mornings, then roamed apart throughout the day. The primary sleep site was in a stand of *Vachellia (Acacia) xanthophloea* at a levee, but both groups used four other sites, exclusively sleeping in the same tree species near seasonal rivers.

Field Experiments

Controlled field experiments were used to measure coping style and stress reactivity. These experiments were part of a broader study and are described more in depth elsewhere (Pritchard & Palombit, 2022a). Briefly, a model puff adder, *Bitis arietans*, was presented to adult olive baboons simultaneously alongside a soft-boiled chicken egg. The egg is an important addition here because the combined experimental set-up with the snake confronts the subject with contrasting stimuli, potentially provoking alternative solutions to the circumstances. These solutions are necessary to quantify coping styles (Koolhaas et al., 1999) and facilitate greater behavioural variation (Réale et al., 2007): whether to confront the stressor and take the egg, a more proactive response, or whether to leave the stressful circumstances without engagement, a more reactive response. Eggs are a natural resource consumed by olive baboons (Barton, 1990). The snake evokes a fear–anxiety response (Carter et al., 2012) and elicits a higher frequency of fear- or anxiety-associated behavioural responses relative to experimental control trials presenting the egg alone; fear-associated behaviours are interpreted as measures of stress reactivity. Coping styles were measured along a quantitative continuum of factor scores that summarized whether individuals confronted the snake to take the egg and, if so, whether they ate the egg and how long it took to do so. Stress reactivity was measured along a continuum of fear-associated grimace frequencies in response to the stimuli.

Behavioural responses to the paradigm were recorded and video data were coded to extract measures of these responses by a coder naïve to the study design but trained to recognize the relevant baboon behaviours. Trials were replicated to obtain intraindividual consistency. Within-trial measures that showed repeatability across trials were reduced into factors using a regularized exploratory factor

analysis (Jung & Lee, 2011). Factor scores were extracted from a single factor to be used as a measure for coping style, which comprised the following measures (in seconds): time spent holding/touching the egg; time spent eating the egg; duration of visual orientation to the snake model after taking the egg; time spent eating egg remnants; latency to eat the egg after taking it (Pritchard & Palombit, 2022a).

More proactive coping individuals are more likely to repeatably take the egg when simultaneously confronted with the stressor, relative to more reactive coping individuals (Pritchard & Palombit, 2022a). Proactive individuals show a lower latency to take the egg, relative to more reactive individuals (Pritchard & Palombit, 2022a). Fear grimaces, a facial visual signal involving upper lip retraction, are repeatable in response to the experimental stimuli and used as a measure of stress reactivity (Pritchard & Palombit, 2022a). Individuals scoring higher stress reactivity show higher frequencies of fear grimaces in response to the stressor, relative to individuals scoring lower stress reactivity. Experimental measures were attained for 32 subjects (25 males, 7 females) in 62 treatment trials.

Observational Data

A.J.P. and two research staff achieved 80% concordance reliability prior to conducting 10 min focal animal follows (Altmann, 1974) on subjects selected from randomly generated sequence lists. A mean (\pm SD) of 129.82 ± 24.20 10 min focal animal samples were collected from 44 individuals, resulting in 982 focal hours. During focal samples, all aggressive, affiliative, submissive and displacement behaviours were collected. For agonism, we recorded a suite of actor–receiver-specific behaviours comprising threats, as well as various forms of physical contact aggression (Ransom, 1972; Strum, 1982). The duration of grooming bouts was recorded directionally (actor–receiver); a change of partners or cessation of grooming for 5 s defined a new grooming bout. If an active grooming bout was in progress during the normal cessation of a focal follow, then the focal was extended until the current grooming bout finished. Spatial association was calculated as the duration a focal individual was in proximity to adults, derived from continuously collected approaches and withdrawals. Two measures of proximity were included: close proximity and social proximity. Close proximity was defined operationally as the space

designated by a 2 m radius around the focal; this was selected for consistency with the present ethogram at the site. Social proximity was designated by a 5 m radius around the focal, selected due to its prior utility in parsing out individual differences in male baboon sociality (Sapolsky & Ray, 1989).

On-site researchers and staff additionally used ad libitum (Altmann, 1974) observations to collect supplementary occurrences of displacements (Bercovitch, 1988). All occurrences of displacements from focal follows and ad libitum observations were used to construct a social dominance hierarchy using randomized Elo-ratings (Sánchez-Tójar et al., 2018), as well as percolation and conductance (P&C) (Fujii et al., 2016; Vandeleest et al., 2016). We assessed certainty (behavioural adherence to the expectations of the hierarchy) and linearity of the hierarchy as recommended by Sánchez-Tójar et al. (2018), using steepness, half-comparisons and dominance transitivity. Elo-rating repeatability provides an estimate of steepness to convey the likelihood that a dyadic interaction adheres to the hierarchical structure contingent on rank distance, with higher steepness indicating greater adherence (Sánchez-Tójar et al., 2018). Dominance transitivity provides a measure of the orderliness of a group and is more robust to null dyads than measures of linearity (McDonald & Shizuka, 2013; Sánchez-Tójar et al., 2018). Randomized Elo-ratings are an extension of the winner–loser scoring system initially developed for chess players (Elo, 1978), but the addition of randomization reduces the emphasis of temporal effects, which would be misleading in this case due to a reliance on a summative rank score rather than rank as a dynamic process. P&C uses a network path approach to infer rank relations between null dyads using the rank relationships of conspecifics. P&C permits a visualization of which dyads have uncertain dominance relationships (Fujii et al., 2016; Vandeleest et al., 2016). Hierarchies were constructed separately for males and females from each group, resulting in four distinct hierarchies: Kati-Kati males, Kati-Kati females, Shire males and Shire females. Although these two groups are of mixed sex and could be examined under a single hierarchy, each sex has a distinct sociosexual and psychosocial nature of dominance hierarchies. For instance, males typically secure rank through contest competition, while females tend to have a matrilineal rank inherited via birth order (Palombit, 2013; Strum, 1982).

<H2>*Ethical Note*

Permissions were obtained for research from the Kenyan Wildlife Service and the National Commission for Science, Technology and Innovation. Approval was also obtained by Rutgers' Institutional Animal Care and Use Committee (Protocol number 16-039). The direct subjects of this study were all adults: 17 female and 27 male subjects distributed across two neighbouring groups totalling 123 group members (90 and 33). Subjects were free-foraging wild olive baboons in Laikipia, Kenya that are monitored as a part of the ongoing 'Project *Papio*'. Disturbance was minimized via long-term habituation of subjects to focal follows. The experimental protocol was frequently replicated without baboons spotting the stimuli, to reduce potential associations between the experimenter (A.J.P.) and the stimuli. Stimuli were similar to threats and incentives that baboons frequently encounter in the field (puff adder snakes and eggs). Eggs were soft-boiled for 1 min in water that had been brought to a rolling boil prior to adding the egg. No invasive samples were collected. No tags were attached or used for these data.

Statistical Analyses

For statistical analyses, we used R (version 4.0.0-2) (R Core Team, 2021) within the RStudio® IDE (version 1.3.959) (RStudio Team, 2018). Adjacency matrices and social network graphs were constructed using the 'igraph' packages (Csárdi & Nepusz, 2006). To assemble social networks, we first calculated adjacency matrices where each actor occupied a row and column; proximity networks were undirected and thus symmetric, while grooming and aggression networks were directed and thus asymmetric. As individuals were unevenly sampled due to conditions of fieldwork (e.g. deaths and disappearances), durations and frequencies were converted into rates based on the observation time for the focal actor before creating the matrix.

To test Prediction 1, we calculated assortativity metrics using the ‘assortnet’ package (Farine, 2014; Newman, 2003). ‘Assortnet’ does not facilitate statistical hypothesis testing, but careful consideration of assortativity coefficients and their standard errors can provide insight into whether heterophily or homophily is expressed. Disassortive heterophily is indicated by negative values, while assortive homophily is indicated by positive values. Standard errors are computed via jackknifing and can be used to give an estimate of confidence as to whether an assortativity value is likely to include a value of 0, indicative of random assortment.

For models Predictions 2a–d and Prediction 3, we started with models that only included the variable of interest as a predictor (coping style), then used both step-up and step-down Akaike information criterion (AIC) ‘step()’ to find a model that maximized explanatory power while minimizing complexity; the retained model was selected with the prerequisite that it would retain the relevant predictors to test each prediction. We included sex, group, rank and all possible interactions between these variables (see Table A1 for more details and AIC results).

For Predictions 2a–c, we conducted node–label permutations using the Animal Network Toolkit Software (‘ANTs’) package (Sosa et al., 2020), with two-tailed tests for significance. For Prediction 2a, we ran a node-permuted Gaussian GLM using the grooming networks with outdegree as a dependent variable to determine whether more proactive coping style factor scores significantly predicted the number of grooming partners, with sex as an additional predictor. For Prediction 2b, we ran a node-permuted Poisson GLMM using the 2 m networks, with degree as a dependent variable to determine whether more proactive coping style factor scores significantly predicted the number of spatial associations. Sex, ordinal rank and an interaction between ordinal rank and coping style score were included as additional predictors, as well as group as a random effect. For Prediction 2c, we ran a node-permuted Gaussian GLM using the aggression networks, with outstrength as a dependent variable to determine whether more proactive coping style factor scores significantly predicted high rates of aggression towards more partners, with sex and ordinal rank as additional predictors.

We used a GLMM model with partner stability indices (PSIs) to test Prediction 2d (Silk et al.,

2012). This analysis first consisted of compiling monthly proximity adjacency matrices, then ascertaining the identity of the top three individuals that each subject was proximate to during each month. Then, we used the formula in Silk et al. (2012), as follows

$$\frac{NS - U}{NS - S} = \text{PSI}$$

where N is the number of months that each subject was present in the data set, $S = 3$, which represents the number of conspecifics we considered to be association partners, and U is the total number of unique conspecifics that an individual associated with throughout the project period. As in Silk et al. (2012), PSI could range from 0 to 1, with 1 signifying that the same three conspecifics were partners throughout, while 0 represents a new top three partners every month. There were 28 adults in Kati-Kati and 16 in Shire; thus, the lowest possible PSI scores would be 0.36 or 0.67, respectively. As such, we rescaled each PSI relative to the group that each subject was in. The final model included the rescaled PSI scores as the dependent variables to determine whether coping style scores significantly predicted stable partner associations. We included ordinal rank as well as an interaction between rank and coping style scores as additional predictors; we also included group as a random effect.

Finally, to test Prediction 3, we used a GLMM to determine whether coping style scores predicted the dependent variable of ordinal rank in males only, with group as a random effect.

RESULTS

Field Experiments

Field experimental results are detailed more fully elsewhere (Pritchard & Palombit, 2022a). The coping style and stress reactivity measures were independent (Pearson correlation: $r = 0.05$; Hoeffding's correlation: $D = -0.02$, $P = 1.00$), in line with theoretical expectations (Koolhaas et al., 1999). Within-

individual repeatability across replicated trials was acceptable for coping style (Spearman rank correlation: $r_s = 0.43$) and stress reactivity (Spearman rank correlation: $r_s = 0.33$). These values are in line with expectations of behavioural repeatability according to meta-analyses of general behaviours (Bell et al., 2009). In the Shire study group, individuals had a mean (\pm SD) coping style score of -0.173 ± 0.77 and mean (\pm SD) stress reactivity of 4.75 ± 7.36 . In the Kati-Kati study group, individuals had a mean (\pm SD) coping style score of 0.001 ± 0.87 and mean stress reactivity of 3.77 ± 5.11 .

Hierarchies

The ratio of interactions to individuals and the proportion of dyads observed interacting suggests that sampling effort was sufficient (McDonald & Shizuka, 2013; Sánchez-Tójar et al., 2018) for estimating each of the hierarchies (Appendix). Additionally, the transitivity and steepness analyses indicated linear dominance structures, albeit with some uncertainty in the male hierarchies. Examination of reversals revealed a lower average proportion of reversals in the P&C method, relative to the randomized Elo-ratings (Appendix). The P&C approach was, therefore, used to compute ordinal rank estimates for the remaining analyses. Because rank certainty was higher in the ends of hierarchy, ordinal rank was retained for analyses. Additionally, despite moderate uncertainty, the dominance transitivity of the networks suggested that they were orderly and that the uncertainty was likely due to violations attributable to individual attempts to alter rank rather than a complete absence of hierarchical structure.

Hypothesis Testing

Assortativity of social networks

We explored whether coping style and stress reactivity variation correspond to group assortativity (Hypothesis 1). Generally, assortativity measures did not support Prediction 1: homophily was not observed in the grooming network along axes of coping style and stress reactivity (Table 1). For the Shire study group, there was moderate heterophily (mean \pm SE = -0.47 ± 0.15) for stress reactivity in the

grooming network.

This heterophily was, however, largely driven by the grooming dynamics of a single highly stress-reactive male. Instead, strong heterophily between the sexes was the dominant pattern of assortativity in the grooming networks (mean \pm SE: Kati-Kati: -0.75 ± 0.06 ; Shire: -0.70 ± 0.09) and 2 m proximity networks (Kati-Kati: -0.34 ± 0.06 ; Shire: -0.45 ± 0.07). While quantitative metrics for assortativity seemed suggestive of heterophily along coping styles in the aggression networks, the estimates were deemed to be uncertain due to high standard errors. In Kati-Kati, there was slight homophily in the aggression network for ordinal social dominance rank (mean \pm SE = 0.19 ± 0.13) and slight heterophily with coping style (-0.23 ± 0.17).

As the proximity network showed high density (Fig. 1, Appendix), we split this network into two networks to gain a better understanding of the structure of the strongest and weakest edges following Croft et al. (2009) and to allow a more fine-tuned comparison. We kept all edges that exceeded the mean edge strength for the ‘strong edge network’, and all the edges below this cutoff were retained in the ‘weak edge network’. The strong and weak 2 m proximity networks revealed finer structural nuance (Table 1). For both groups, relative to the complete 2 m proximity networks, heterophily in sex was maintained and more pronounced in the strong edge network but lost in the weak edge network. We found that the strong edge networks exhibited moderate homophily for coping styles (mean \pm SE: Kati-Kati: 0.21 ± 0.08 ; Shire: 0.27 ± 0.21). Additionally, there was some indication for heterophily via stress reactivity in the strong 2 m network for Shire (mean \pm SE = -0.19 ± 0.10). The weak 2 m network did not show homophily; rather, in Shire, there was heterophily for coping style (mean \pm SE = -0.41 ± 0.07). Ordinal rank was a poor metric of assortativity in the strong and weak edge 2 m networks.

In summary, the group assortativity in the grooming network did not support homophily with coping style or stress reactivity; however, in the strong edge 2 m network, we did observe homophily via coping style for both study groups. This suggests that individuals may preferentially associate with conspecifics that share a similar coping style.

Social network position

We examined whether individual coping style influences the expression of sociality (Hypothesis 2) (Wolf & Krause, 2014). Our predictions (Predictions 2a, 2b, 2c and 2d) were not supported. Relative to reactive individuals, more proactive individuals did not have more grooming partners (measured via outdegree: GLM Gaussian: coping style: estimate: -0.02, confidence interval, CI: -0.01, 0.05, $P = 0.81$), did not associate spatially with more partners (measured via degree: GLMM Poisson: coping style: estimate: 0.001, CI: 0.0004, 0.001, $P = 0.06$) and did not aggress upon more individuals at higher rates (measured via outstrength: GLM Gaussian: coping style: estimate: 0.003, CI: -0.0004, 0.0005, $P = 0.73$; Table 2). Although no predictions were made regarding the other independent variables, grooming was not commonly performed by males, as evidenced by males' substantially lower outdegree in the grooming networks than females. Finally, it was generally observed that males had significantly higher outstrength in aggression networks than females (Table 2). Overall, social network position of individuals, as measured by the relative number and strength of prosocial, spatial and agonistic interactions, did not covary systematically with coping style. Male and female baboons, however, differed significantly in grooming and aggression, with females grooming more dyadic partners than males did, while males aggressed upon either more individuals or with a greater frequency than females, or both (Table 2). Spatial associations showed similar trends but not significantly.

Relative to more proactive individuals, more reactive coping individuals did not spend more time associating with the same conspecifics throughout the study period, measured via PSI (GLMM Gaussian: estimate for coping style: -0.14, CI: -0.47, 0.20, $R^2 = 0.26_{\text{marginal}}$; Table 3). Although no predictions were made regarding the other variables, it was generally observed that high-ranking individuals had higher PSI, signifying greater partner stability, relative to low-ranking individuals.

Social dominance hierarchies

We examined whether consistent individual differences in response to a stressor are associated with individual rank as the outcome of agonistic interactions (Hypothesis 3). We found no evidence to

support our Prediction 3: male coping style did not vary with social status (GLMM Gaussian: estimate for coping style: -0.74, CI: -2.76, 1.40, $R^2 = 0.01_{\text{marginal}}$; Table 3).

DISCUSSION

Our study found only partial support for individual differences in coping style or stress reactivity to affect assortativity in wild olive baboon social groups: spatial associations, evidenced through a proximity network, showed some homophily in coping style. Individual positions within their social groups, as quantified via centrality measures in several behavioural networks, were not predicted by coping style, nor were individual social ranks. Below we discuss why assortativity for coping style might only be weakly expressed. We then emphasize why our findings diverge from findings of covariance of social position and individual differences in birds, possibly due to the strong stable group structure of olive baboons. Finally, we provide directions for future research on the social consequences of consistent individual differences in the stress response system and recommend focusing on life history stages defined by high uncertainty or rapid decision making; we emphasize that dynamic feedbacks likely exist between social group compositions, interactions and individual behaviours themselves.

Assortativity of Social Networks

We found homophily in coping style only when the weaker edges of a proximity network were excluded and the stronger edges were retained. However, we found no support for homophily in coping style or stress reactivity in any other network. This result supports other studies of primates reporting similarly equivocal findings either for particular subgroupings (Massen & Koski, 2014), across groups, or through time (Carter et al., 2015). In lieu of direct comparisons on assortativity with coping style and stress reactivity in primates, we can only examine assortativity with other personality traits. Although Massen and Koski (2014) found homophily in boldness, this relationship was limited to social associations among nonkin. In great tits, Johnson et al. (2017) reported homophily with boldness for

breeding nest placement among males, but not among females. Other axes of variation in assortativity may need to be considered when examining variation in personality-based assortativity.

Although not a specific focal point of our study, our findings of heterophily in sex parallel those in chacma baboons (Carter et al., 2015), but in the present study, assortativity was much stronger than in chacma baboons. This is notable as, despite a higher prevalence of infanticide in chacma baboons (Palombit, 2003; 2012), males and females in both allotaxa form heterosexual friendships, especially prominent during periods of lactation (Palombit et al., 2001; Shur, 2008; Smuts, 1982). Such friendships provide a potential behavioural rationale for strong heterophilic patterns. Heterophily in sex was also observed in mixed-sex groups of red-fronted lemurs, *Eulemur rufifrons* (Sperber et al., 2019). This parallel finding is interesting because these lemurs have also been reported to exhibit special male–female relationships similar to olive and chacma baboon friendships (Overdorff, 1998; Pereira & McGlynn, 1997). Future research on assortativity in these taxa may benefit from explicit incorporation of friendships or consortships, the latter of which are also male–female associations, albeit more temporary.

Social Network Position

Of the four predictions regarding the association between coping style and social network position, none was of sufficient statistical significance to be supported by our results. This contrasts with studies on birds, which have reported significant relationships between coping style and network position (Aplin et al., 2013; Moyers et al., 2018; Snijders et al., 2014). Our findings are more in line with those reported in meerkats, *Suricata suricatta*, by Pacheco (2020), who found no relationship between individuals' network positions and two personality traits, aggressiveness and friendliness, across 15 groups and three networks: dominance, foraging competition and grooming. Pacheco (2020) suggested that positive publication bias could account for associations of previous personality traits and social network position. Alternatively, it is possible that the smaller networks of meerkats and olive baboons do not allow the social choice afforded by flocking behaviour in birds. Similar to olive baboons, individual

meerkats occupy relatively large mixed-sex social groups with dominance hierarchy structures (Clutton-Brock et al., 2006), within which individuals use submissive signalling and avoidance (Kutsukake & Clutton-Brock, 2008). Meerkats and olive baboons maintain strong temporal and spatial associations that provide high-quality information about conspecifics, without the necessity to interact. That is, individuals gain information on conspecifics through observation of third-party interactions, which may not be a possibility in species that break associations for brief or extended periods through their life cycle, such as in great tits. Indeed, baboons attend longer to experimental playbacks of calls that signify violated expectations for rank structure (Cheney et al., 1995). Perhaps coping style differences would have more predictive value during periods of greater social uncertainty. Indeed, this is the conclusion that Carter et al. (2013) derived from observing foraging behaviours at experimental food patches with varying certainty of quality: boldness predicted behaviour during these experimental sessions but not during natural feeding.

Alternatively, it could be that the use of centrality measures, such as strength or degree, relies too heavily on structural complexity and, instead, using triadic scales, motif-based analyses or simplicial sets (Silk et al., 2022; Wang et al., 2020) would be more appropriate for complex and consistent social groupings. For example, Kalish and Robins (2006) reported that individuals with tendencies to exert control or who have higher neuroticism will bridge more transitive connections. Thus, the reports of higher degree for proactive individuals might reflect small local differences in interactions, as the proactive coping style is characterized by tendencies to attempt to exert control over stressful circumstances (Coppens et al., 2010; Verbeek et al., 1999).

The partner stability indices (PSIs) covaried with social dominance rank, such that higher-ranked individuals had more stable associations across the study months. Even though this was not a tested prediction, this result is surprising given that previous studies on baboons did not find an association between PSI and rank (Seyfarth et al., 2012; Silk et al., 2012). A salient distinction between these studies is the inclusion of males in the present study. As such, this indicates that females and males may have been competing for spatial associations during this study. This could be juxtaposed to the female-only

bonds, whereby females are reliant on kin-based relationships (Silk et al., 2012). Post hoc exploratory models on the present dataset suggest that rank effects on PSI are stronger in males than in females, and this finding may suggest that the effects of PSI in males reflect consistent associations via friendships or consortships secured through rank-based priority of access.

Social Dominance Hierarchies

Despite relying on the coping style continuum, we found a similar null relationship to rank in concordance with studies using other personality-like traits, including: boldness (Carter et al., 2012; 2015; Ray & Sapolsky, 1992; Sapolsky & Ray, 1989; Seyfarth et al., 2012; Virgin & Sapolsky, 1997). The consistency of such null relationships is perhaps surprising given that rank is not solely an emergent social property of the group but is influenced by individual attributes (Chase et al., 2002; Sapolsky, 2005). It might be, instead, that personality traits are only significant in male baboons during key demographic or life history stages, such as the process of coordinating (soliciting or joining) coalitions or dispersal. For instance, variation in cerebrospinal fluid 5-hydroxyindoleacetic acid (CSF 5-HIAA, a metabolite of serotonin) is associated with variance in dispersal age in rhesus macaques (Higley et al., 1992; Kaplan et al., 1995; Trefilov et al., 2000). This is relevant as CSF 5-HIAA levels have been associated with increased risk taking and impulsivity (Higley et al., 1992; Trefilov et al., 2000) and is a significant biomarker for stress reactivity or coping style variation (Koolhaas et al., 2010).

Coalition formation might also be influenced by coping style as heightened social responsiveness in more reactive coping individuals (Aplin et al., 2013; Coppens et al., 2010; Snijders et al., 2014; van Oers et al., 2005; Wolf et al., 2011) could aid in coordinating actions with conspecifics (Wolf & Krause, 2014). This expectation might be observed in baboons via reactive individuals soliciting or joining coalitions more frequently and effectively than proactive males, who might rely on more confrontational strategies. Using the current data set, we examined whether the raw frequency of coalitions that individuals solicited or joined were correlated with coping style scores. These exploratory analyses

suggest, contrary to this expectation, that more proactive individuals were more likely to join (Pearson correlation: $r_{28} = 0.21$) or solicit ($r_{33} = 0.35$) aggregated defensive, aggressive and supporting coalitions. Neither reactive nor proactive individuals were more likely to be the target of aggregate coalitions ($r_{30} = 0.002$). Coalitionary behaviour, however, can be dynamic, and these aggregated data neither accurately reflect temporal complexity or interaction dynamics, nor fully parse out the distinct contexts over which coalitions may form.

The Individual Within

Our null results for rank and social position variables do not support covariance in the metrics of social structure and coping style in a wild primate. This outcome is surprising given the growing theory of social consequences to coping style variation (Aplin et al., 2013; Moyers et al., 2018; Snijders et al., 2014; Verbeek et al., 1996, 1999). Many of these studies, however, involved birds. This is a relevant consideration because the general nature of a given taxa inevitably interplays with patterns and tendencies of social structures. Indeed, comparisons of six metrics of network structure in a repository of 45 species revealed that mammalian network metrics clustered along with fish and insects, in contrast to birds (Sah et al., 2019). This finding calls into question the utility of the significant findings reported in avian species for informing the dynamics of personality and social structure in wild primates. For instance, great tits form aggregated associations only during nonbreeding seasons, with groupings characterized by a fission–fusion structure during this time (Aplin et al., 2013). Interestingly, Massen and Koski (2014) reported homophily among the associations formed in chimpanzees, a species that also has a fission–fusion society, although their subjects were captive.

Baboons cannot escape their current group's composition without emigrating or dispersing into another group. Given the strong associations of baboons, future research should consider whether group composition might limit the individual variance that subjects express, based on the personality of other group members or other metrics of social structure. Prior evidence suggests that such social constraints

are likely. For example, while relatively more asocial mosquitofish, *Gambusia affinis*, are generally more likely to disperse than more social conspecifics, an individual is also more likely to disperse if its group is composed of a relatively higher proportion of conspecifics that score higher in boldness or lower in sociality, irrespective of the individual's score (Cote et al., 2011). Consequently, we propose that the rules of baboon group social structures are rigidly enforced and, as such, individuals are restricted from expressing particular behaviours, contingent on the individual differences of conspecifics within the group.

Even amidst a rigid societal structure, personality-like trait associations likely still have a role in influencing social dynamics but simultaneously tend to be limited by current social structure. For example, experimental manipulations of rhesus macaque social dominance structure resulted in changes in behavioural tendencies of boldness and social approachability but not anxiety (Kohn et al., 2016). Thus, altered social structure created a new situation (Clifton, 2014); situations can alter measures of personality but do not invalidate personality as a construct (Funder, 2006; Pritchard et al., 2014; Uher et al., 2008). Assuming this framework to be true, we recommend a greater focus towards dynamic frameworks that quantify the rigidity that social structure establishes on individual behaviours, while also investigating the behavioural flexibility that individuals can exhibit across time and group structures. For instance, McCowan et al. (2008) documented that, in captive rhesus macaques, matrilineal structure, kinship memberships and sex ratio of a group predicted aggression and injury as well as hierarchical certainty. The same research group, however, also found that personality traits predicted the propensity for individuals to intervene in third-party conflicts, an integral trait for maintaining group stability (McCowan et al., 2011). Such findings synergize group level attributes with individual level nuance, which likely dynamically interact.

There is also a growing recognition that personality-like individual differences might be more fruitfully conceptualized in network approaches, as opposed to traditional latent or operational models (Goold, 2020; Martin et al., 2019). Such an approach is gaining momentum in human psychology, which acknowledges the complexity of context specificity and dynamic expression as well as latent and

observed variation (Goold, 2020). Irrespective of the statistical approach, it is this complexity that must simultaneously be acknowledged and statistically accounted for if we hope to understand the function and stability of consistent individual differences. For instance, our experimental paradigm might have inadvertently sampled individuals at contextually incomparable periods, even though we implemented numerous control conditions to minimize such occurrences. Alternatively, we might not have captured all underlying variables of interest to quantify coping style variation. Indeed, the presence of heightened behavioural flexibility in reactive individuals (Coppens et al., 2010) would predict that more reactive individuals show greater intraindividual variation (Stamps et al., 2012) across situations, relative to the more consistent or predictable proactive individuals. This expectation creates problematic expectations about what repeatability is (how can individuals defined by increased variability be repeatable?) and the influence of increased information obtained through inhibited decision making. Finally, other personality traits likely interact with the shifting social landscape, facilitating or constraining the influence of individual differences in coping style and stress reactivity.

<H2>Conclusion

Only one of the variables of interest was associated with coping style differences: strong connections in a 2 m proximity network showed homophily via coping style differences. Coping style did not predict social dominance position or individual social network centrality measures (i.e., degree or strength centrality). Possibly, using higher-resolution analyses to isolate particular situations, contexts or substructures (e.g. transitive closures) might provide a stronger capacity to resolve the role of individual differences within a long-term social group structure. For instance, primate personality traits are probably more informative in decision making when individuals have little certainty about their environment (Carter et al., 2013). As Hinde emphasized: ‘interactions influence, and are influenced by, relationships and thus by social structure’ (Hinde, 1976, p. 3), and individual traits are ‘independent or intervening variables’ (Hinde, 1976, p. 2). We extend this logic to emphasize, however, that such traits are also

mutable or constrained with respect to group structure. If we know that individual differences interact with group structure as a dynamic process, then elucidating the ramifications of this phenomenon is extraordinarily challenging without controlled manipulation of group composition or structure itself. This provides a compelling direction for theoretical modelling studies or controlled captive experiments to continue to develop in future research.

Author Contributions

A.J.P. was responsible for all aspects of the project including conceptualization, formal analysis, funding acquisition, investigation/data collection, project administration and writing – original draft.

A.J.C. contributed to conceptualization, study design, and writing – review & editing. R.A.P. contributed to conceptualization, funding acquisition, study design, project administration, supervision, writing – review & editing as well as project infrastructure and its associated funding.

Data Availability

Data is available through DataDryad at <https://doi.org/10.25338/B8M350>. Any additional data from relevant publications are available from the corresponding author upon reasonable request.

Declaration of Interest

None.

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Appendix

Hierarchies

Metrics of hierarchy structure are presented in Table A2. The ratio of interactions to individuals and the proportion of dyads observed interacting suggests that sampling effort was sufficient for estimating each of the hierarchies (McDonald & Shizuka, 2013; Sánchez-Tójar et al., 2018). Even long-term studies are unlikely to observe all dyads interacting, due to bystander observations, knowledge of conspecific rank relations and avoidance that can occur beyond 2 mrs (Cheney & Seyfarth, 1999; Cheney et al., 1995; McDonald & Shizuka, 2013). Nevertheless, every individual performed or received a displacement with at least one other conspecific.

Sánchez-Tójar et al. (2018) recommended an Elo-rating repeatability cutoff of 0.70. In the Kati-Kati study group, the female hierarchy had very high steepness (0.92), evidence of hierarchical certainty, but the male hierarchy showed only moderate steepness (0.68). Both male and female hierarchies in Shire had moderate steepness (0.72 and 0.78, respectively). Half comparisons were also conducted, which compute whether two halves of the dominance data are concordant; values exceeding 0.35 indicate linear hierarchical structure. All of the hierarchies exceeded this cutoff. The Kati-Kati female hierarchy had high and significant ($P < 0.001$) transitivity (1.00), suggesting that this hierarchy was orderly. In line with the half comparisons, Shire group and Kati-Kati group males had less orderly hierarchies. Kati-Kati male and Shire female hierarchies were still significantly ($P < 0.05$) transitive (0.62 and 0.60, respectively), while the Shire male hierarchy transitivity (0.59) trended towards significance ($P = 0.053$). Together, the transitivity and steepness analyses indicated linear dominance structures, albeit with some uncertainty in the male hierarchies. Metrics of sampling adequacy suggest that the data were sufficient in quantity and, instead, it is likely that uncertainty is a factor of this system, rather than a product of the data.

Estimated ranks were largely similar between the randomized Elo-ratings and P&C methods. Confusion matrix heatmaps of each P&C hierarchy revealed greater uncertainty between dyads in the

central positions of all of the hierarchies, i.e. mid-ranking individuals. These results support the mild instability of the Shire group and the moderate instability in the Kati-Kati male hierarchy. Instability of hierarchies has historically been demonstrated via the proportion of reversals to interactions that individuals exhibit within the hierarchy; i.e. how many instances individuals violate the expectations of the hierarchy (Gesquiere et al., 2011; Sapolsky, 1992). Reversals (Table A2) substantiated the previous methods, with the proportion of reversals highest in the Kati-Kati male hierarchy, followed by Shire males and Shire females, while Kati-Kati females had the lowest proportion of reversals. Examination of reversals revealed a lower average proportion of reversals in the P&C method, relative to the randomized Elo-ratings. The P&C approach was, therefore, used to compute ordinal rank estimates for the remaining analyses. Because rank certainty was higher in the ends of hierarchy, ordinal rank was retained for analyses. Additionally, despite moderate uncertainty, the transitivity of the networks suggested that they were orderly and that the uncertainty was likely due to violations attributable to individual attempts to alter rank rather than a complete absence of hierarchical structure.

Structures of Social Networks

Several metrics can be used to assess general group structure (Table A3) for each of the social networks. The proximity networks were generally defined by high density scores (Prell, 2012; Wasserman & Faust, 1994); that is, the networks had edges connecting almost all of the nodes (98–99%). We quantified density (Prell, 2012; Wasserman & Faust 1994) via the ‘edge_density() igraph’ function. This signifies that all possible baboon dyads within the groups were observed in close proximity over the course of the study. Centralization scores (Prell, 2012), a measure of whether particular nodes are responsible for the majority of connections in a network, were obtained via the ‘centr_degree() igraph’ function. The obtained centralization scores (Prell, 2012) indicated that these networks were not contingent on a few influential individuals. Density of the grooming and aggression networks were very different, with only 11–30% of potential ties existing within the networks. This signifies that the

grooming and aggression networks were sparser than the proximity networks and that the majority of dyads did not interact with aggressive or grooming behaviours. While the centralization scores of these latter two networks were higher than the proximity networks, they were not heavily centralized via a few influencers. Kati-Kati and Shire differed slightly in density scores, but density can be influenced by network size. Because centralization scores are influenced by network size, we also extracted the longest geodesic paths/unweighted diameters and average path lengths (Prell, 2012) using the ‘diameter()’ and ‘mean_distance()’ functions in ‘igraph’, respectively. The longest geodesic paths/unweighted diameters and average path lengths were similar for the proximity networks across the groups. The grooming and aggression networks also had similar diameters and path lengths across the study groups. Thus, patterns of connectivity were similar across the groups, with differences in density likely attributable to network size rather than to social structure. Transitivity metrics (Prell, 2012; Wasserman & Faust, 1994) suggested slightly more complete closure in the Shire’s grooming and aggression networks. For instance, triads in the Shire were more likely to all have groomed each other throughout the study period, relative to triads in the Kati-Kati group, where there may not be triadic closure. Transitivity metrics (Prell, 2012; Wasserman & Faust, 1994) were extracted using the ‘transitivity()’ function in ‘igraph’. Random walk communities (Pons & Latapy, 2005) revealed some potential subgroups in all of the networks, except for the two Shire proximity networks. Random walk communities (Pons & Latapy, 2005) were extracted using the ‘walktrap() igraph’ function.

As the individuals of Kati-Kati and Shire often ranged together and interacted, we also computed social network metrics for the large composite group (‘Both’ in Table A3). Generally, these unified social networks showed trends across the different behavioural networks similar to those observed in the single group networks. The unified networks, however, were more diffuse, reflecting the divide between the major subgroupings (Kati-Kati and Shire). Although there were some associations between the groups, random walk community analysis of the united proximity networks reinforced the distinct social units of Kati-Kati and Shire, which were delineated based on patterns of subjective assessments of clustering and roaming during the study period, as well as daily censuses.

We compared transitivity of the complete proximity networks to values in the ‘strong edge’ and ‘weak edge’ proximity networks. Relative to the complete and weak edge networks, transitivity was lower in the strong edge network for Kati-Kati, but not for Shire (Table A3).

To quantify the degree of similarity between the different behavioural networks, we used the K_r test (Hemelrijk, 1990) via the ‘stat.tauKr() ANTs’ function (Sosa et al., 2020). We computed network correlations using the K_r test (Hemelrijk, 1990). Across the grouping structures, the aggression network showed poor correspondence to the other networks (mean τK_r : 0.04, $N = 6$), excluding the united proximity networks where there was a weak positive correlation for the 5 m and 2 m networks ($\tau K_r = 0.23$ and 0.24 , respectively). The proximity networks showed moderate to strong positive correlations with each other (τK_r : minimum = 0.48, maximum = 0.87). Finally, both proximity networks showed moderate positive correlations with the grooming networks (τK_r : minimum = 0.35, maximum = 0.51).

Table A1

Akaike Information Criterion (AIC) stepwise model selection

Model	Steps	+/- Variable	Step Df	Dev.	Resid. Df	Resid. Dev	AIC
P2a	1	(base model)	NA	NA	30	210.30	157.06
	2	+ Sex	-1	64.89	29	145.42	147.26
P2b	1	(base model)	NA	NA	30	340.23	172.46
	2	+ Sex	-1	125.83	29	214.39	159.68
	3	+ Group	-1	19.50	28	194.89	158.63
	4	+ Rank (ordinal, scaled) + Coping style (scaled)	-1	19.27	27	175.62	157.29
	5	: Rank (ordinal, scaled)	-1	11.12	26	164.50	157.20
P2c	1	(base model)	NA	NA	30	0.04	-113.61
	2	+ Sex	-1	0.01	29	0.03	-120.90
	3	+ Rank (ordinal, scaled)	-1	<0.01	28	0.03	-122.58
P2d	1	(base model)	NA	NA	30	34.66	99.37
	2	+ Rank (ordinal, scaled) + Coping style (scaled)	-1	6.55	29	28.12	94.67
	3	: Rank (ordinal, scaled)	-1	2.01	28	26.10	94.29
P3	1	(base model)	NA	NA	23	766.09	162.51
	2	+ Group	-1	208.95	22	557.14	156.55

Table A2

Metrics for steepness and certainty of dominance hierarchies

	Kati-Kati		Shire	
	Female	Male	Female	Male
Interaction ratio	11	15.4	12.1	15.4
Proportion known dyads				
Observed	0.82	0.63	0.81	0.87
Expected Poisson mean (CI)	0.61 (0.36–0.89)	0.49 (0.34–0.66)	0.65 (0.36–0.95)	0.65 (0.39–0.95)
Uncertainty				
Elo repeatability	0.92	0.68	0.78	0.72
Half comparison	0.80 (0.55–0.95)	0.45 (0.14–0.73)	0.55 (0.02–0.90)	0.53 (0.02–0.90)
Transitivity	1.00***	0.62***	0.60*	0.59†
Correlation of randomized Elo vs P&C ranks	0.97	0.81	0.9	0.74
Proportion of reversals mean (min.– max.)				
Randomized Elo	6.71% (0.00–15.63%)	24.61% (4.35–54.55%)	19.49% (5.88–33.33%)	19.19% (8.33–27.27%)
P&C	5.47% (0.00–15.63%)	21.90% (4.35–39.13%)	15.32% (5.88–29.63%)	19.42% (8.33–33.33%)

Percolation and conductance (P&C) uses ordinal ranks calculated using percolation and conductance. Numbers in parentheses represent

confidence intervals for the relevant metrics. † $P = 0.053$; * $P < 0.05$; *** $P < 0.001$.

Table A3

Metrics of social structure across numerous social network types and groupings

Network type	Group	Grooming	2 m proximity			5 m proximity	Aggression
			Weak edges	All edges	Strong edges		
Density (centralization)	Kati-Kati	0.17 (0.27)	0.72 (0.20)	0.99 (0.01)	0.26 (0.33)	1.00 (0.00)	0.11 (0.13)
	Shire	0.30 (0.32)	0.57 (0.37)	0.98 (0.02)	0.42 (0.32)	1.00 (0.00)	0.18 (0.17)
	Both	0.11 (0.17)		0.62 (0.31)		0.66 (0.30)	0.07 (0.08)
Unweighted diameter (average path length)	Kati-Kati	4 (2.14)	2 (1.28)	2 (1.01)	4 (1.92)	2 (1.00)	6 (2.82)
	Shire	4 (1.82)	2 (1.43)	2 (1.02)	3 (1.57)	1 (1.00)	5 (2.19)
	Both	8 (3.04)		2 (1.38)		2 (1.34)	9 (3.66)
Transitivity	Kati-Kati	0.28	0.74	0.99	0.37	1.00	0.26
	Shire	0.49	0.59	0.98	0.54	1.00	0.38
	Both	0.34		0.81		0.82	0.28
Random walk communities	Kati-Kati	4	3	3	3	4	8
	Shire	3	3	1	4	2	7
	Both	7		2		2	9

Table 1

Metrics of social structure across numerous social network types and groupings

Group	Grooming	2 m proximity			5 m proximity	Aggression
		Weak edges	All edges	Strong edges		
Sex						
Kati-Kati	-0.75 (0.06)	-0.04 (0.05)	-0.34 (0.06)	-0.52 (0.07)	-0.17 (0.05)	0.07 (0.06)
Shire	-0.70 (0.09)	0.13 (0.10)	-0.45 (0.07)	-0.61 (0.07)	-0.21 (0.08)	0.19 (0.11)
Rank						
Kati-Kati	-0.01 (0.08)	-0.04 (0.05)	-0.01 (0.05)	-0.08 (0.06)	-0.03 (0.04)	0.19 (0.13)
Shire	-0.08 (0.18)	-0.06 (0.10)	-0.09 (0.10)	-0.10 (0.13)	-0.15 (0.08)	-0.03 (0.22)
Coping style						
Kati-Kati	0.03 (0.12)	-0.06 (0.06)	0.09 (0.05)	0.21 (0.08)	0.00 (0.05)	-0.23 (0.17)
Shire	0.06 (0.30)	-0.41 (0.07)	0.08 (0.17)	0.27 (0.21)	0.03 (0.13)	-0.17 (0.33)
Stress reactivity						
Kati-Kati	0.01 (0.12)	-0.04 (0.06)	0.01 (0.06)	0.05 (0.12)	-0.01 (0.06)	0.00 (0.12)
Shire	-0.47 (0.15)	0.06 (0.14)	-0.12 (0.08)	-0.19 (0.10)	-0.13 (0.07)	-0.13 (0.15)

For each network type, we present assortativity values, ranging from -1 to 1 (heterophily to homophily, respectively), and the standard error, in parentheses.

Table 2

Statistical models for Predictions 2a, 2b and 2c

	Estimate	SE	<i>t</i>	<i>P</i>			CI			
				Left	Two-sided	Right	Lower	Mean	Upper	
P2a: Gaussian GLM										
Grooming out degree centrality ~ sex + coping style (scaled)										
<i>N</i> =32										
(Intercept)	6.703	0.844	7.938	0.999	0.002	0.001	3.985	4.040	4.096	
Sex (Males)	-3.420	0.956	-3.578	0.001	0.002	0.999	-0.083	-0.011	0.060	
Coping style	-0.090	0.401	-0.223	0.405	0.810	0.595	-0.008	0.021	0.050	
Null deviance: 208.97, <i>df</i> =31; residual deviance: 144.22, <i>df</i> =29										
P2b: Poisson GLMM										
Proximity (2 m) degree centrality ~ sex + rank (ordinal, scaled) + coping style (scaled) + sex:rank (ordinal, scaled) + (1 Group)										
<i>N</i> = 32; groups = 2										
Random effects										
Group (Intercept)		Variance	SD							
		0.08	0.28							
Fixed effects										
		Estimate	SE							
(Intercept)		2.998	0.231	13.010	0.758	0.484	0.242	2.991	2.991	2.992
Sex (Males)		-0.013	0.124	-0.105	0.089	0.178	0.911	0.004	0.005	0.006
Rank		-0.021	0.163	-0.130	0.038	0.076	0.962	0.006	0.006	0.007
Coping style		0.012	0.039	0.312	0.968	0.064	0.032	0.000	0.001	0.001
Interaction of sex (Males): rank		0.033	0.172	0.193	0.983	0.034	0.017	-0.004	-0.003	-0.002
P2c: Gaussian GLM										
Aggression out strength centrality ~ sex + rank (ordinal, scaled) + coping style (scaled)										

(Intercept)	0.002	0.013	0.167	0.000	<0.001	>0.999	0.0359	0.0360	0.0370
Sex (Males)	0.053	0.015	3.655	>0.999	<0.001	0.001	-0.001	0.0000	0.0006
Coping style	0.003	0.006	0.470	0.636	0.728	0.364	0.0004	0.0000	0.0005
Rank	-0.010	0.006	-1.849	0.057	0.114	0.943	0.0000	0.0000	0.0008
Null deviance: 0.05, <i>df</i> =31; residual deviance: 0.03, <i>df</i> =28									

CI: confidence interval. *P* values signify whether observed values fell outside of expectations based on node level permutations, and confidence

intervals are presented as a metric of effect size.

Table 3

Statistical models for Predictions 2d and 3

	Variance	SD	<i>t</i>	CI	
				Lower	Upper
P2d: Gaussian GLMM					
Partner stability indices (scaled) ~ coping style (scaled) + rank (ordinal, scaled) + coping style (scaled):rank (ordinal, scaled) + (1 group)					
<i>N</i> = 32; Groups = 2					
Random effects					
Group (Intercept)	0.03157	0.1777			
Fixed effects					
(Intercept)	Estimate	SE			
	-0.06	0.22	-0.26	-0.36	0.29
Coping style	-0.14	0.18	-0.81	-0.47	0.20
Rank	-0.50	0.17	-3.03	-0.79	-0.17
Interaction of coping style:					
Rank	-0.26	0.18	-1.44	-0.61	0.08
$R^2_{\text{marginal}} = 0.26$; $R^2_{\text{conditional}} = 0.29$					
P3: Gaussian GLMM					
Rank (ordinal, scaled) ~ coping style (scaled) + (1 group)					
<i>N</i> = 25; groups = 2					
Random effects					
Group (Intercept)	Variance	SD			
	18.5	4.301			
Fixed effects					
(Intercept)	Estimate	SE			
	7.27	3.24	2.24	-0.65	14.93
Coping style	-0.74	1.03	-0.71	-2.76	1.40
$R^2_{\text{marginal}} = 0.01$; $R^2_{\text{conditional}} = 0.43$					

CI: confidence interval. For these GLMM models, confidence intervals are a metric of significance and R^2 values are presented as a metric of effect size.

Figure 1. Social network graphs across various behaviours and for each group. Grooming and aggression networks are directed with edges being read in a clockwise direction. Proximity network graphs (2 m and 5 m) are undirected. Males are shown in gold, females are shown in magenta; node sizes are a function of degree. Edge colours are determined by a blended colour from the sex of the dyad, with pink signifying a mixed-sex dyad. This figure was made using Gephi (Bastian et al., 2009).