Nutritional needs and social bonds: how early-life dependencies shape meerkat sociality

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Lay Summary

Social bonds in wild meerkats are driven by nutritional needs and learning opportunities during periods of cooperative pup care. We found no evidence of long-term benefits from maintaining strong individual relationships beyond nutritional dependency periods. Instead, meerkats maintain a level of general gregariousness, interacting with all group members at an even propensity, once their young achieve nutritional independence.

Abstract

Across species, social systems vary in their extent of interactions, competition, cooperation, and cohesion. Though there has been considerable research on overall social structures, the dynamics of how an individual's social niche develops during early life and how biological needs of offspring shape sociality has received less attention. In this study, we took a longitudinal approach targeting the developmental period from nutritional dependency to independent foraging, and toward sexual maturity, to assess within-group sociality of a cooperative mammal, wild Kalahari meerkats (*Suricata suricatta*). First, we used a novel approach to disentangle individual-specific from dyad-specific tendencies to interact to characterize social within-group dynamics during foraging. Second, we then used these two sociality features to identify formation of social relationships during early development. By combining proximity scans with data on social interactions from focal follows, we investigated the biologically relevant behaviours driving the observed social interactions. Our results show that meerkat sociality is generally highly dynamic with respect to dyadic relationships. The strength of dyadic relationships between pups and adults was highest during pups' nutritional dependence and was positively linked to pup-care behaviors initiated by both adults and pups themselves, while such dyadic relationships decreased in strength after nutritional independence. During early ontogeny, meerkat pups rely heavily on food provisions for survival and learning of their species-specific diet to develop their independent foraging skills. As such, our findings indicate that social relationships in meerkats are a by-product of the socio-ecology of cooperative pup care and lack a need for long-term individualized relationships.

Keywords: Social ontogeny, meerkats, sociality, dyadic interactions, gregariousness, foraging needs, nutritional dependence

Definitions

Dyadic Affinity: Propensity of two individuals to interact with one another

Gregariousness: Overall propensity to interact with another conspecific

Ethics

All data collection for this study has been conducted under the ethics and research permits held by the Kalahari Meerkat Project (University of Pretoria Ethics Permit, NAS003/2022; Research Permit from the Northern Cape Province Department of Environment and Nature Conservation, South Africa, FAUNA 0930/2022), as well as ethics and research permits held by the Meerkat Cognition Project (University of Pretoria Ethics Permit, NAS061/2022; Research Permit from the Northern Cape Province Department of Environment and Nature Conservation, South Africa, FAUNA 0931/2022), and has not adversely impacted the health or well-being of the individuals being studied.

Introduction

Social systems across the animal kingdom present dynamic networks reflecting ecological pressures and flexibility over time (Alexander 1974; Ebensperger et al. 2012; Salguero-Gómez 2024; Ward and Webster 2016). Also, within species social traits and their links to fitness varies among individuals, according to rank, sex and age (Hobson and DeDeo, 2015; Sadoughi et al. 2024; Siracusa et al. 2022; Thompson González et al. 2021; Wooddell et al. 2020). Yet, little is known how developmental trajectories determine individual social niches. Some studies have explored how social complexity and stress experienced in early ontogeny impacts social positioning and therethrough later life reproductive success (White et al. 2010; Boogert et al. 2014), but few studies have taken a longitudinal approach to investigate the development of an individuals' social position and behavior over time, and how ontogenetic needs relate to the wider group networks. When this has been done, studies often rely on cross-sectional comparisons between different age classes, failing to produce the stronger level of inference that longitudinal studies can provide (Brown 2017; Woodman et al. 2024). Cross-sectional studies provide a series of static snapshots that limit our ability to capture the intricate processes of social development and relationship formation and maintenance. Such methods are often

applied because some species long life histories make longitudinal studies difficult (Isler and van Schaik 2012; Salguero-Gómez 2024), or due to the limitations of bio-loggers in capturing relevant data where direct observation is not possible (Resheff et al. 2016).

In typically competitive social species, including primates such as rhesus macaques (*Macaca mulatta*) and other mammals such as African elephants (*Loxodonta africana*), where social groupings are composed of multiple-breeders, hierarchies, or fission-fusion dynamics, it has been found that offspring inherit social connections from their mothers. This can have benefits for their survival, while later-life selectivity of relationships can bring other benefits in old-age, such as formation of allies (Ilany and Akçay 2016; Maestripieri 2018; Siracusa et al. 2022; Siracusa et al. 2022; Whiten 2017). Cooperative single-breeder systems are often overlooked, especially with limited evidence of long-term individualized relationships (Dunbar 1998; Salguero-Gómez 2024). However, cooperative systems could drastically differ from competitive ones in their socio-ecological pressures resulting in sociality impacting developmental processes distinctively. For example, across closely related woodpecker species (*Picidae spp*.) that differ in their social organization, comparative work suggests that competitive and cooperative social systems have different cognitive requirements, reflected in brain size differences, where social stability may select for reduced brain size (Fedorova et al. 2017). As such, cooperative social systems may differ to competitive social species in their demands for individualized relationships.

Additionally, studies of animal sociality typically focus on behavioral contexts such as resting, as this is when our perception of the most social behaviors like grooming and play are expressed, and since these behaviors reportedly facilitate formation and maintenance of long-term social bonds (Diamond and Bond 2003; Hodgson et al. 2024; Kutsukake and Clutton-Brock 2010; Lazaro-Perea et al. 2004; Pellis et al. 2023; Preston et al. 2021; Reinhart et al. 2010; Schino et al. 1988). However, social relationships are also important in other contexts, such as foraging, which take up large portions of activity budgets. In many group-living and/or cooperative species, the foraging context involves behaviors such as resource provisioning, communication, and potential social learning, all known to interact with offspring development (Agostini and Visalberghi 2005; Hintz and Lonzarich 2018; Thornton 2008; van Boekholt et al. 2021).

Most studies on sociality have thus far focused on describing network positioning of individuals (Barocas et al. 2011; Boogert et al. 2014; Madden et al. 2011; Turner et al. 2021; Zonana et al. 2021), or pairwise relationships (Razik et al. 2022; Ripperger and Carter 2021; Silk et al. 2013; Stockmaier et al. 2020; Wyman et al. 2021). However, more recent studies have begun to explore the benefits of broadening methods

to combine behavioral, spatial, and life-history measures when constructing animal social networks (Davis et al. 2018; Kaburu et al. 2023; Sosa et al. 2021). Doing so could improve our understanding of how sociality is developed, maintained, and is intertwined with both early-life survival and lifetime fitness (Armitage 2012; Barocas et al. 2011; Boogert et al. 2014; Brent 2015; Dakin et al. 2021; Drewe 2009; Hobson and Carter, 2022). Furthermore, to uncover any ecological relevance and changes in sociality over time, new approaches emerge with the scope to disentangle two sociality features: *dyadic affinity* (the propensity of two individuals interacting preferentially with one another specifically) and the individual level of *gregariousness* (the propensity of an individual to interact with any other conspecific) (Neumann and Fischer 2023). This methodology deviates from typical approaches by explicitly disentangling mechanisms underlying observed dyadic interactions, allowing a more fine-grained assessment of social structure. For example, this approach was recently used to model food transfers in Guinea baboons (*Papio papio*) (O'Hearn et al. 2024). In this study, the size of subgroups ('audience') around food owners correlated positively with the food owner's gregariousness, while the composition of the audience and the identities of individuals that food was transferred to mapped on the dyadic affinity feature (O'Hearn et al. 2024).

In this study, we used this framework to examine the ontogeny of sociality in a cooperatively breeding mongoose, meerkats (*Suricata suricatta*). Meerkats live in highly cohesive groups in semi-arid zones of the Kalahari and surrounding regions of Southern Africa. Groups are typically composed of 2-50 individuals including a dominant pairing and subordinates who are usually their offspring (Clutton-Brock et al. 2004, 2006; Griffin et al. 2003; Russell et al. 2006). In meerkats, within group social networks have been shown to vary greatly between individuals and across different types of social interactions (grooming, dominance interactions, and foraging competition) (Madden et al. 2009, 2011). Meerkat sociality also appears to become less dense as group size increases, which has led to the idea that individuals may be limited in the number of connections that they can make and maintain (Madden et al. 2009), which may imply limitations in socio-cognitive skills or time budget constraints. Previous analyses based on social proximity during foraging revealed that meerkat social connectedness vary over time and do not reflect a consistent network (Gall and Manser 2018). Thus far, however, this research lacks ontogenetic effects, and one could predict that the presence of pups impacts sociality within groups in cooperative species, since cooperative care of young represents a key trait of their social system.

We used a longitudinal study design to characterize within-group sociality and social development in meerkats. We focused on the two distinct features of sociality proposed by Neumann and Fischer (2023) –

the *gregariousness* of individuals, and *dyadic affinity* – to disentangle how meerkat pups develop their sociality during early life and the overall social characteristics of meerkats groups. In this methodological framework, when variation in individual gregariousness is low and variation in dyadic affinity is high, the structure of the social system is likely driven more by the interplay of each individual's dyadic preferences than by each individuals' overall interaction propensity, and vice versa (Neumann and Fischer, 2023). We therefore hypothesized that due to the cooperative and cohesive nature of meerkat societies, maintaining similar levels (i.e. little variation) of gregariousness across individuals will be necessary to enable groups to succeed and persist. Furthermore, greater differentiation (i.e. large variation) in the pair-wise relationships within a group (dyadic affinities) predictably would reflect the dynamic within-group structure. Consequently, we expected to find smaller variation in gregariousness compared to dyadic affinities.

To identify the role of early development in shaping social relationships in meerkats, we investigated whether social relationships (dyadic affinity) of pups change throughout their ontogeny. More precisely, we were interested in variation in overall propensities to interact in general (gregariousness) or with specific adults (dyadic affinity), and how developmental trajectories may impact the overall group social structure. To do so, we targeted data collection to seven developmental time points across three critical transition periods spanning meerkat ontogeny: from early reliance on provisioning, to nutritional independence, and up to the approach of sexual maturity. We hypothesized that when pups first begin to leave their native burrow system to join the group while foraging, their social interactions would be highly dynamic and indiscriminate but become more selective towards the most cooperative adults as they age and can identify and act upon provisioning opportunities. Beyond the point of nutritional independence, we expected low variability in how differentiated dyadic relationships are due to the limited evidence of individualized relationships in previous adult-focused studies (Gall and Manser 2018; Madden et al. 2009, 2011).

Lastly, we aimed at identifying the biologically relevant behaviors that are driving the social niche of meerkat pups. We asked whether pup-adult relationships based upon proximal associations during foraging are driven by adult-initiated food provisioning behavior, or pup-initiated following interactions, which encompasses looking for and maintaining close proximity to adults to maximize chances of receiving food. Adult meerkats do not show specific roles in pup-care but vary in their overall cooperation (Clutton-Brock et al. 2001, 2003). Moreover, it has been reported that adults are more likely to feed pups that are closer in proximity to them and those pups that are emitting the loudest begging calls (Manser and Avey, 2000). Consequently, we hypothesized that both adult-initiated provisioning and pup-initiated following interactions

will be positively correlated to proximal associations. We suggest that it would be more beneficial for pups to form stronger relationships with the adults providing the greatest levels of care. It would therefore be reasonable to suggest that pups with these socio-cognitive skills may position themselves in close proximity to favored adults to increase their likelihood of receiving provisioning, whether from a single or even several adults.

Methods

Study site & species

The study was conducted at the Kalahari Research Centre (KRC), situated at the Kuruman River Reserve in the Northern Cape of South Africa (26°58'S, 21°49'E). This long-term study site covers a semi-arid habitat of the Southern Kalahari region including the fossilized dunes surrounding the dry riverbed of the Molopo River, of which the Kalahari Meerkat Project has been based since 1993 (for full information on the meerkat study system, see Clutton-Brock and Manser 2016). Our study took place between October 2022 and June 2024 and covers data from two successive breeding seasons (October to March). To assess social development of meerkat pups, we collected detailed focal follows (Altmann 1974) and social scan data on 31 meerkat pups representing 8 litters (litter size ranging from 3 – 5) from 7 different groups (group size ranging from 11 – 29) across the two breeding seasons. To be able to detect any ontogenetic changes, we adopted a longitudinal approach across the first year of the pups' lives. Thus, for each pup we collected data at 7 time points hereby referred to as data weeks (Figure 1). These cover three points in the three months prior to nutritional independence (approximately 12 weeks of age), with four points covering the subsequent 9 months of development as they acquire nutritional independence and approach sexual maturity and adulthood at approximately one year of age (Figure 1). For data weeks 5 – 10, data within the 7 days prior and 6 days after reaching that age point were assigned to the relevant data week. For data weeks 13 – 24, data within 14 days prior and beyond the relevant age point were considered. For data at 1-year of age, data within the 30-days prior the pup's first birthday, and any data for the following year was considered for this data point. These boundaries were put in place to account for some minor variability in planning the data collection in the field with a limited field team of a maximum of two persons at any given time.

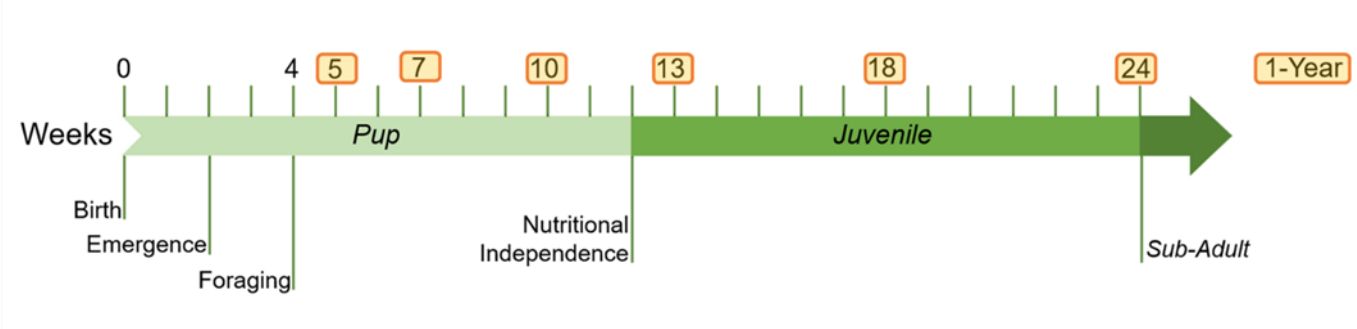

Figure 1: Timeline of meerkat pup ontogeny with major developmental transitions (noted in text). Highlighted week numbers, and 1-year of age, are the points of study interest (data weeks).

Focal data collection

The primary source of behavioral observation used in this study was focal follows conducted on the pups of interest. For the first breeding season (October 2022 – July 2023) the adult individuals within the study groups were also followed to target group-wide social measures. Individuals were closely followed by an observer between 1-2m for 20 minutes. This resulted in 210.2 hours of focal data collected, across 8 litters from 7 groups, and a breakdown of this data can be found in the supplementary materials, Table S1. All behaviors during this period of the focal individual were recorded continuously. All focal follows were conducted by trained researchers using Blackview BL8800 smartphones with a bespoke data collection form using Pendragon software (version 2.316A). An ethogram of the behaviors from these focal follows used within this study can be found in the supplementary materials, Table S2.

Scan data collection

We collected proximity data during foraging, noting the nearest neighbor identity and distance for each of our focal individuals through scan sampling. For the first breeding season (October 2022- July 2023), the entire group was sampled with each individual within the group having their closest conspecific group member's identification and distance recorded while the group is foraging, at intervals of at least 20 minutes. In total, 571 scans with nearest neighbor measures of the entire group were collected, covering the 3 groups of interest in the first season, with a total of 84 individuals, thereof 11 pups. This dataset entailed an average of 29 scans per group (and therefore 29 nearest neighbor measures per individual) per data week. During the second breeding season (October 2023 – June 2024) – due to time constraints – nearest neighbor data was only collected for the pups of primary interest, and therefore nearest neighbor data was not available for the entire group. Instead, data was collected via 'circle scans' whereby the group is scanned regarding each

individual's distance to the focal pup, gaining the nearest neighbor to the pup as well as distances of other group members to the pup of interest within 10m. In total, 1,179 circle scans were conducted across the 5 groups, targeting the 20 pups from this breeding season. These were conducted at an average of 30 scans per group per data week, with a target of 15 scans (and therefore 15 nearest neighbor measures) per individual pup at each data week. Similarly to focal follows, all scan sampling was conducted by trained researchers using Blackview BL8800 smartphones with a bespoke data collection form using Pendragon software (version 2.316A).

Quantifying Sociality

For the aims of the study, we analyzed three types of social behavior during foraging contexts: *proximity* was the identity of the nearest neighbor individual (based on distance and collected from scan sampling), *adult-initiated interactions* were considered as pup-feeding events where food is provisioned by an adult towards a pup or juvenile, and *pup-initiated interactions* were considered as active close-following interactions between a pup or juvenile and an adult (within 2m, with the pup maintaining visual contact and the same movement direction as the adult).

Proximity and adult-initiated pup-feeds were processed as frequency of occurrence between all possible dyads. Pup-initiated interactions were treated as the duration of time a focal pup followed another individual. We used a Bayesian modelling approach implemented by the '*bamoso*' R-package (Neumann and Fischer, 2023). This method allows for proximity and interaction frequency and duration matrices to be modelled alongside matrices of relevant observation effort in estimating individual- and dyad-level sociality values. In the proximity measures, observation effort was calculated as the maximum number of instances each pair of individuals could have been recorded as nearest neighbors, based upon individual sightings within the groups at a data collection point. For both behavioral interaction measures, observation effort was the maximum focal follow duration of which each pair of individuals could have had interactions recorded between them. This was calculated based upon the duration of individual focal follows and the presence of other individuals during that observation session. For the longitudinal study of the proximity values alone at a group-level, matrices were constructed based upon proximity measures from the entire group for the first breeding season pups (Table S1: NN count including and excluding pups). To be able to make comparable models between the different sociality measures (proximity and behavioral interactions), and to explore individual variation between-pups in sociality, matrices were constructed using only interactions involving

pups of interest for the entire dataset (Table S1: NN count including pups, and total group focal hours). Any interactions between pups, or between other individuals within the group were not considered in these latter analyses.

The '*bamoso*' model estimates two features of sociality, resting on the assumption that dyadic interactions and associations are driven by both *individual gregariousness* as well *dyadic affinity* (Neumann and Fischer, 2023). Based upon an observed behavior of a count measure such as how often two individuals were proximally associated, this can be expressed as follows:

$$y_{ij} \sim \text{Poisson}(\lambda_{ij})$$

$$\exp(\lambda_{ij}) = b + \sqrt{0.5}(g_i + g_j) + r_{ij} + log(E_{ij})$$

$$g \sim N(0, \sigma_g^2)$$

$$r \sim N(0, \sigma_r^2)$$

Where y_{ij} is the observed frequency of interactions between individuals i and j. λ_{ij} is the positive rate parameter of a Poisson distribution that is determined by b, g, r and E. b is the intercept term of the expected propensities of two individuals with average gregariousness and average dyadic affinity, g is the individual sociality (gregariousness), r is the dyadic sociality (dyadic affinity), and E is the observation effort. For simplicity, we omitted the prior specifications from the equation. The model estimates the variance of individual (σ_g^2) and dyadic (σ_r^2) propensities to interact or be within proximity from the observed data. In addition to group-level measures of variability in individuals and dyads, we can extract the actual propensities for each individual and dyad, and these can then be used in further statistical analyses and network approaches. Furthermore, exploring the variation (standard deviation) in the values of individual gregariousness and dyadic affinity allowed us to assess the weight of each feature of sociality within a population.

To assess whether a measure of sociality is correlated with another, an adaptation of this model can allow for several interaction types to be modelled together, and correlation coefficients among the underlying affinity and gregariousness features to be estimated as follows (example with two behaviors):

$$y_{ij} \sim \text{Poisson}(\lambda_{ij})$$

$$w_{ij} \sim \text{Poisson}(Y_{ij})$$

$$\exp(\lambda_{ij}) = b_y + \sqrt{0.5}\left(g_{y_i} + g_{y_j}\right) + r_{y_{ij}} + log\left(E_{y_{ij}}\right)$$

$$\exp(Y_{ij}) = b_w + \sqrt{0.5}\left(g_{w_i} + g_{w_j}\right) + r_{w_{ij}} + log\left(E_{w_{ij}}\right)$$

$$g_y \sim N\left(0, \sigma^2_{g_y}\right)$$

$$g_w \sim N\left(0, \sigma^2_{g_w}\right)$$

$$r_y \sim N\left(0, \sigma^2_{r_y}\right)$$

$$r_w \sim N\left(0, \sigma^2_{r_w}\right)$$

$$\rho^g_{yw} = cor(g_y, g_w)$$

$$\rho^r_{yw} = cor(r_y, r_w)$$

Where y_{ij} and w_{ij} are the observed interactions between i and j for two behaviours (e.g. proximity and adult-initiated pup-feeds, recording as frequencies and modelled as Poisson distributed). As above, this model estimates both the variance of individual (σ^2_g) and dyadic (σ^2_r) propensities to interact or be within close proximity from the observed data but here separately for each of the behavioral interaction or proximity types, while simultaneously estimating the correlation coefficients. In other words, for two behaviors y and w, we estimate one correlation (ρ^g_{yw}) for gregariousness and one correlation (ρ^r_{yw}) for dyadic affinity. With three behaviours, we obtain three gregariousness correlations and three affinity correlations between all possible pairs.

Statistical analyses

To consider the relationships between the quantified sociality measures and developmental time from the resultant posteriors, Bayesian multilevel hierarchical models were used. To first compare the focal pups' individual- and dyad-level sociality values with the rest of the group over their developmental time, we used the nearest neighbor proximity data from the groups studied in the first breeding season (Table S1, NN measures both including and excluding pups). For the analyses of the dyadic affinity values, the response variable of mean dyadic affinity across all possible dyads from all estimated posteriors, was fitted against the explanatory variables of the studied developmental data weeks (as a scaled continuous time variable) and a binary explanatory variable of whether each dyad included a focal pup of interest or not. An interaction term was added to assess for any potential difference in longitudinal effect on whether the dyad included a pup or

not ("PairType"). To account for the potential effect of developmental time varying between individuals, random slopes for time in individuals were included. We fitted a multi-membership model to handle the arbitrariness in assigning individuals IDs in dyads. This resulted in the following model formula: affinity ~ time * PairType + (time || mm(Individ1, Individ2)), where affinity is the posterior mean for affinity from the output of the bamoso model.

In analysis of gregariousness, mean gregariousness for each individual from all estimated posteriors was fitted as the response variable against the studied developmental data weeks (as a scaled continuous time variable), along with whether the individual was a focal pup of interest or not ("IndividType"). Again, to account for the potential effect of developmental time changing between individuals, a random slope for time was included with the random effect of individual identification. Resultant formula = gregariousness ~ time * IndividType + (time || IndividCode). In both models, we used a non-centered parametrization approach. Due to the hierarchical structure of our data (84 individuals across 3 groups) and the relatively small variance components relative to observation noise detected in initial models and data exploration (common in behavioral data with high individual variation), this technique was chosen to improve sampling. LOO (leave-one-out) cross validation model comparison and posterior predictive checks assisted in our model selection of using a non-centered parametrization, as well as consideration of the random slope of time with our random effect. Furthermore, model comparison showed that group identity did not account for any further residual variation that was not already accounted for with the individual identity and therefore was excluded in the final model which also improved convergence and removed all divergence issues.

To identify any possible link between the different sociality measures (proximity and behavioural interactions), we extracted correlation coefficients estimated in '*bamoso'* models between measures for both gregariousness and dyadic affinity (equation 2, line 280 - 289). These analyses are based on comparing pups on their social values, with matrice– centered around the interactions that included at least one pup without consideration for adult-adult interactions. For this purpose, proximity and focal follow data from the full study period of both seasons was used (Table S1: NN measures (incl. pups) only, and Group Focal Hours; Total dyads considered: n = 489). There were three pairwise correlations between different affiliative behavioral matrices generated from the models that were analysed: proximity and following interactions (pup-initiated), proximity and pup feed interactions (adult-initiated), and between following and pup feed interactions (considered as overall pup-care). It should be noted that due to occurrence of pup-care behaviors reducing considerably in their frequency beyond the point of nutritional independence (~ 12 weeks of age), as well as

the birth of the next litter (when younger pups were present in the groups resulting in focal individuals contributing to the care of such pups rather than being recipients beyond this point) we only looked at correlation coefficients between these interactions up to Week 13. This was to ensure a suitable sample size of data and avoid incorrectly interpreting interactions relating to the care of pups not otherwise included in this study.

All statistical analyses were done in R (v. 4.3.3, R Core Team, 2024). Models were fitted with the *bamoso* package (Neumann and Fischer 2023) and *brms* package (Bürkner 2017).

Results

Comparing two features of sociality

Variation in gregariousness was lower than variation in dyadic affinity with standard deviations for gregariousness across groups ranging between 0.05-0.25 and standard deviations for affinity ranging between 0.25 to 0.85 (Figure 2). Therefore, dyadic affinities are typically more differentiated than individual gregariousness values. At the individual level of all pups, the standard deviation of dyadic affinity remained higher than that of gregariousness at all data weeks with similar longitudinal trends (Figure S1). However, the data also indicated that individual variation exists as to the actual mean values of dyadic affinity and gregariousness, both within- and between-groups (Figure S1).

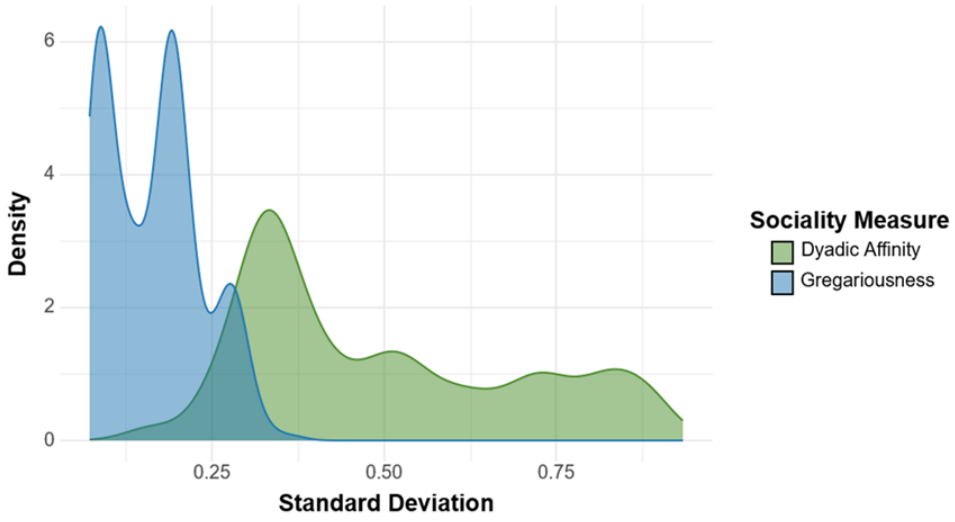

Figure 2. Density plot of standard deviation values of gregariousness and dyadic affinity of all individuals and dyads. Calculated by *bamoso* modelling of proximity social measures, aggregated for the entire study period. The densities represent aggregated posterior distributions over time points and groups.

Developmental changes of sociality: affinity

Dyadic affinity showed temporal changes across early development (Figure 3.A, numerical results are in Table 1), but this pattern differed between pair types. Average dyadic affinities decreased for pairs which included pups (purple in Figure 3.A), while for pairs without pups (orange in Figure 3.A), we found a slight increase over time. In addition, at the youngest age, i.e., shortly after emergence when pups start foraging, average affinities were higher in pairs with pups compared to pairs without pups, and this pattern was reversed once pups were sexually mature.

Table 1: Numerical results for affinity model.

	Estimate	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	0.05	0.01	0.08	1.00	7508	5919
Data Week (z-transformed)	-0.06	-0.11	-0.01	1.00	7766	6624
Pair Type Other (reference: with pups)	-0.02	-0.05	0.01	1.00	17447	9516
Interaction (Week:Pair Type)	0.07	0.03	0.11	1.00	13549	8908

Developmental changes of sociality: gregariousness

We did not observe any notable temporal trends or differences between pups and adults in their average gregariousness (Figure 3.B, Table 2), i.e., gregariousness appeared to be stable over time and similar in pups and others.

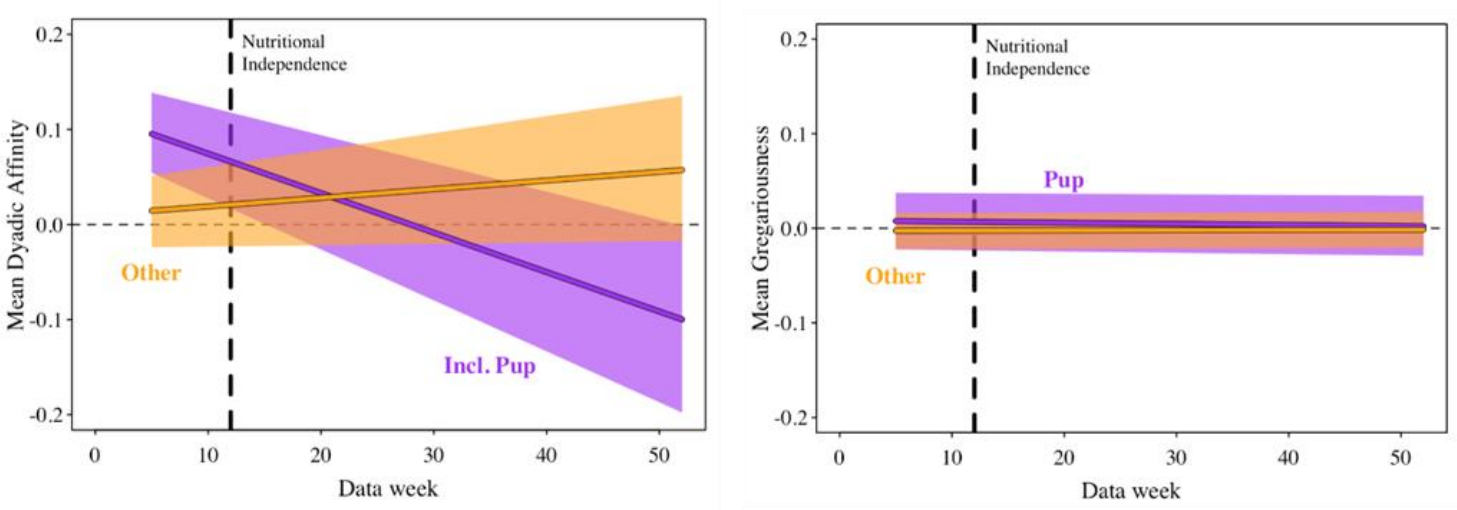

Figure 3. Temporal variation in (A dyadic affinity and (B) gregariousness values between pups and other group members. 'Pup' refers to the focal individuals of interest that were pups at the start of the study, with the data weeks referring to their age. 'Other' includes all older individuals in the group. Values of 0 are the point of reference of a mean dyadic affinity or gregariousness value at the group level. Shading in both plots represents the 95% confidence intervals of the posterior means of individuals within the pair or individual type, with data points and lines representing the overall mean of posterior values of each pair or individual type. Data covers 84 individuals - 11 of which are pups - and all possible dyads from 3 groups.

Table 2: Numerical results for gregariousness model.

	Estimate	l-95% CI	u-95% CI	Rhat	Bulk_ESS	Tail_ESS
Intercept	0.00	-0.03	0.02	1.00	5388	4010
Data Week (z-transformed)	0.00	-0.03	0.03	1.00	6768	6277
Individual Type Pup (reference: other)	0.01	-0.03	0.04	1.00	13168	9063
Interaction (Week: Individual Type)	-0.02	-0.07	0.03	1.00	12892	9628

Developmental changes of sociality: maintenance of pup-adult dyads over time

To evaluate whether any pup-adult dyadic relationships were maintained over time, we calculated Pearson correlation coefficients of pup-adult dyads between consecutive data weeks which confirmed small positive correlations between the posterior means of strength of dyadic affinity of pup-adult dyads at Week 5 to Week 7, Week 7 to Week 10, and Week 13 to Week 18 (Figure 4). A small negative correlation was found between Week 10 to Week 13, and correlations near 0 were present between Week 18 to Week 24, and between Week 24 and yearlings (one-year of age, sexual maturity) (Figure 4).

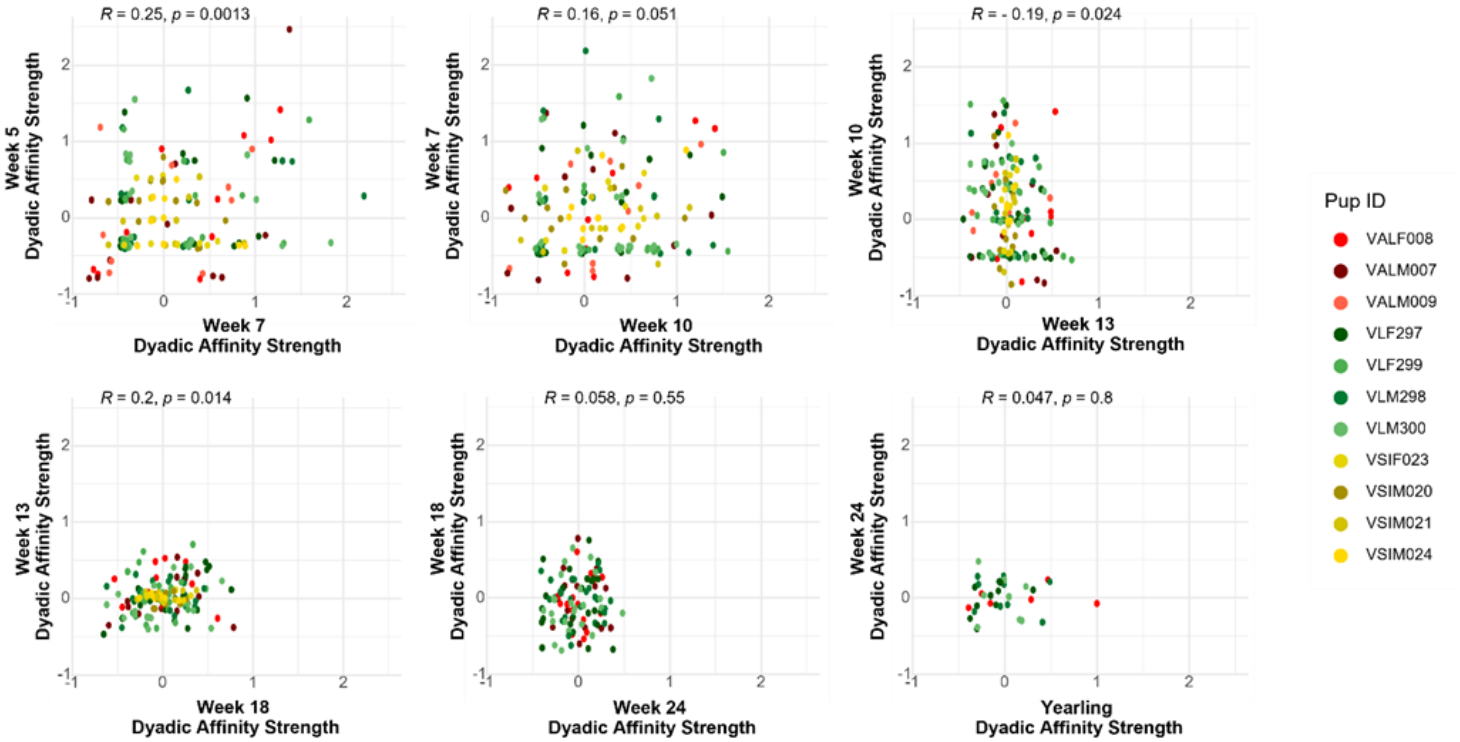

Figure 4. Pearson's correlation coefficients of the strength of dyadic affinity values of pup-adult dyads between consecutive data weeks of 11 pups across the studied period, where specific dyadic pairings are present in both consecutive weeks. Identification of the pup included in the dyads identified by color, with similar shades representing group identity (reds = Alba, greens = Lazuli, yellows = Side Quest).

Correlative measures of sociality between interaction types

We estimated small positive correlations between dyadic affinities for all three pairs of behaviors prior to nutritional independence (most posterior medians ~ 0.2, Figure 5). After the point of nutritional independence, these were much closer to zero. All correlation estimates were associated with considerable uncertainty. In contrast, the estimated corresponding correlation coefficients for pairs of gregariousness were consistently much closer to zero (most posterior medians between 0 and 0.1, Figure 5). These estimates were also associated with large uncertainties.

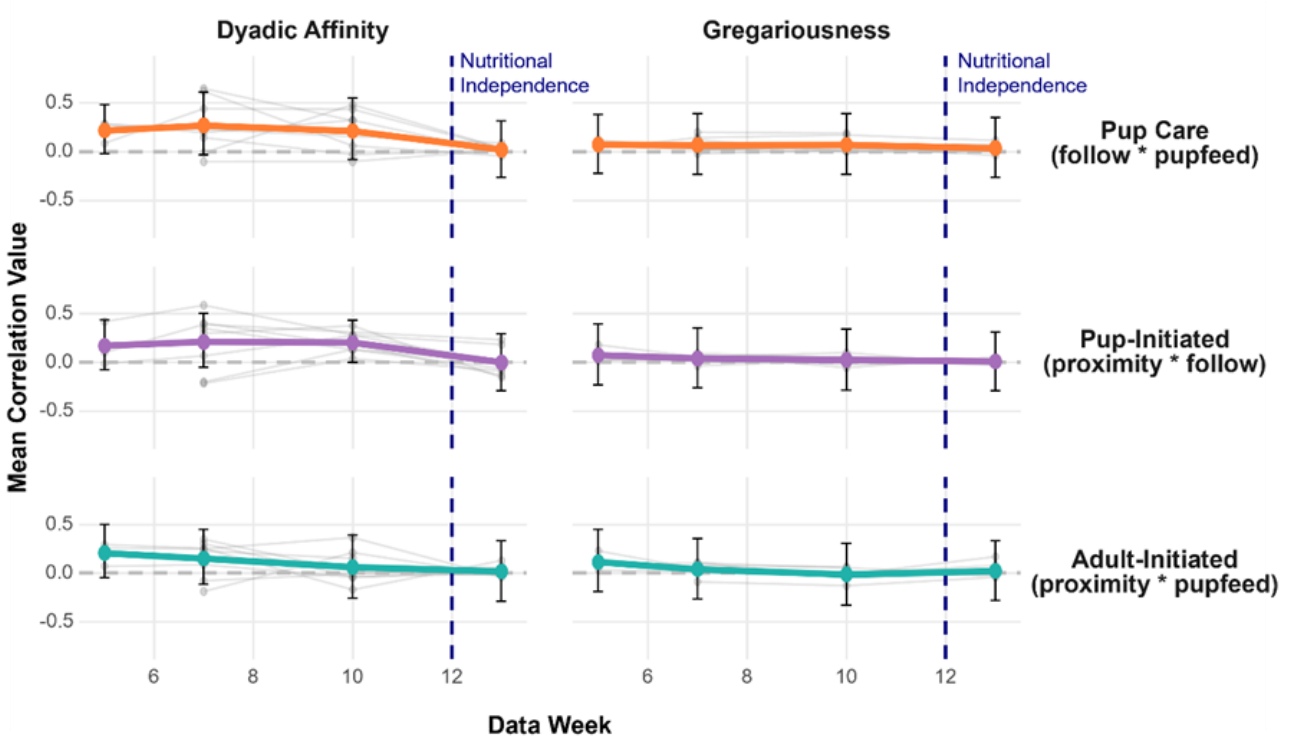

Figure 5. The change in correlation coefficients between sociality measures (dyadic affinity and gregariousness) generated from different behavioral interactions. The mean correlation value indicates the strength of the correlation from posterior correlation coefficients generated with *bamoso* models. Colored points and lines represent the overall mean posterior value for each behavioral correlation, with light grey lines representing the mean posterior for each litter of interest. Error bars represent the interquartile range of the full posterior correlation coefficient values. 'Pup Care' is the correlation between sociality values generated from pup-feeding and following interactions, 'Pup-Initiated' is the correlation between proximity and following interactions, and 'Adult-Initiated' is the correlation between proximity and pup-feeding interactions.

Discussion

In this study, we quantified meerkat sociality up to early adulthood by adopting a new framework, which rests on the assumption that dyadic interactions are the outcome of two latent features dyadic affinity (propensity for two individuals to preferentially interact) and individual gregariousness (propensity of individuals to interact with any other conspecific). We found that a meerkat's social dynamics during foraging

is better described by variation in dyadic relationships, rather than by individual differences in their gregariousness, which showed little fluctuation over the time a group is raising pups (Figures 2 & 3). This result aligns with the expectation that maintaining a similar level of gregariousness across the entire group, helps meerkats maintain their high cohesiveness necessary for their cooperative social system. With the knowledge that cohesive decisions in meerkats such as movement speed and direction are determined through quorums with no clear common initiator (Bousquet et al. 2011), our findings further reinforce that maintaining stable propensities to interact with any individual in a group can allow for such quorums to be successful. Moreover, since meerkat groups show high within-group relatedness (Griffin et al. 2003), we expect there are limited genetic confounding factors on the within-group social structure. However, it may be that the observed limited variability in gregariousness could reflect high relatedness within-groups. White-nosed coatis (*Nasua narica*), a species with fission-fusion dynamics, present consistent sub-grouping patterns which are strongly driven by relatedness rather than any other studied ecological, social, or physiological factors (Grout et al. 2024). This implies that quantifying sociality in terms of underlying mechanisms, could be critical for greater understanding of the influence of demographic factors such as relatedness on these mechanisms across taxa, and enable greater comparability.

After we established how these two sociality features are represented within the social system of meerkats, we explored how both dyadic affinity and gregariousness change over early development. In particular, we were interested in exploring the greater variation found in dyadic affinities, and whether such variation becomes more prominent depending on the nutritional needs of developing pups. We identified that when meerkat groups have pups, dyads including pups declined in their affinity over developmental time, showing heightened dyadic affinity strength prior to the point of first independent foraging around pups' age of 12 weeks, and decreased after pups reach nutritional independence (Figure 3.A.). This contrasts with other dyads in the group, which had a lower affinity prior to pups reaching nutritional independence that thereafter increases slightly over time. Thus, our findings suggest that in meerkats, dyadic relationships are most important early during ontogeny when dyadic interactions between pups and adults are critical for survival, as they ensure pups with sufficient food from provisioning and simultaneously provide critical learning opportunities necessary to acquire foraging independence.

Dyad-level affinities were positively correlated prior to nutritional independence but not thereafter. Meanwhile, for gregariousness, all individual level tendencies to interact were independent of each other. Pup-initiated following interactions maintain a weak positive correlation for a longer duration through

nutritional dependence than adult-initiated pup-feed interactions which become closer to zero at 10 weeks of age, prior to nutritional independence (Figure 5). However, all these estimates were associated with considerable uncertainty and hence must be taken as preliminary. This provides an initial suggestion into exploring further whether pups may play a greater role in driving proximal associations than adults.

A plausible explanation is that the trends in the strength of dyadic affinities (Figure 3.A.) prior to nutritional independence could link to weaning conflict, as found across taxa with parental care (Berger 1979; Bánszegi et al. 2017; Paul and Bhadra 2017). Adults may be energetically limited in their ability to provision beyond their offsprings' most critical developmental periods, while pups developing their foraging skills resulting in many failures, may still attempt to optimize nutritional support from provisioning for an extended time period to maximize growth and/ or skill development. As such, it is plausible that there is a conflict of interest between pups and adults regarding provisioning amounts. Meerkats reach adult-level asymptotes of foraging skills at a similar point to their sexual maturity and morphological asymptotes of growth, suggesting physiological constraints on foraging ability (Duncan et al. in press). Therefore, particularly after their initial early provisioning phase, once pups are in greater control of their movements to develop their foraging skills and efficiency, maintaining close proximity to adults for extended periods could provide necessary learning opportunities. This learning could be driven by cognitive or other trait differences in how adults direct their own proximity positioning towards pups to facilitate social learning, or perhaps more likely based on our initial results, from differences in the social cognitive capability of the pups themselves to direct their own attentiveness to provisioning adults (Figure 5). Further research of pup and adult success in foraging, and their ratio of given and received provisions, alongside fitness measures, would need to be explored to fully understand this process.

While no specified individual relationships have yet been described in meerkat studies targeting adults, we here explored whether any shorter-term evidence of such was present during the early developmental period. We did identify a more specified network from strengthened dyadic affinities between pups and adults. From calculating correlation coefficients of dyadic affinity strength of pup-adult dyads across consecutive studied data weeks, we found small positive correlations between the strength of specific dyadic relationships prior to the peak at 10 weeks of age in relationship strength of pups and adults. Thereafter, we found that these factors correlated negatively across the point of acquiring nutritional independence at approximately 12 weeks of age (Figure 4) before levelling off at correlations of around 0. Overall, this suggests a general trend of heightened correlation in maintaining a strengthened dyadic relationship during

494 nutritional dependence and key learning periods, which becomes negligible beyond this point. This suggests
495 that any specification of relationships between individual meerkats is restricted to early development, and
496 there is no maintenance of such relationships beyond this period.

497 We also note that in periods where there are pronounced stronger dyadic affinities (seen from darker
498 green in Figures S2 – S4), there appear to be equally weaker dyadic affinities (seen from darker red in Figures
499 S2 – S4), specifically identifying adult-adult dyads as presenting an opposing trend to strengthened pup-adult
500 dyads during nutritional dependence (Figure 3). As such, while our results therefore align with previous
501 suggestions that meerkats perhaps have a limitation in the number of strengthened connections that they
502 maintain (Madden et al. 2009), we provide some evidence that this may be more likely due to energy
503 limitations and ecological necessity of such relationships featuring pup dependency on adults rather than
504 socio-cognitive limitations. This is further reinforced by finding limited effect of group size on the trends of
505 dyadic affinity and gregariousness across developmental time, although this would benefit in being confirmed
506 through further analyses including a greater sample of groups differing in size. Instead, our results suggest
507 dyadic relationships are closely related to survival and diet learning, represented in the variation in the
508 strengthened relationships during pup dependency. Although short-term, the sociality during this critical
509 developmental period might have fitness impacts for both individuals and groups.

510

511 Conclusions

512 Overall, we conclude that meerkats present a social system that is driven more strongly by their dyadic
513 affinities, than their individual gregariousness. Trends in their dyadic affinities indicate that dyadic
514 relationships in meerkats are byproducts of the socio-ecological needs of cooperative pup care, necessary
515 for survival and diet learning in this cooperative species, and as such show limited need for long-term
516 individualized relationships. Whilst within-group interactions are highly dynamic with no long-term dyadic
517 relationships, specified associations and short-term maintenance of relationships appear when there are
518 nutritionally dependent pups in a group, which do not stretch beyond the juvenile period.

519 Zooming into a typically less-social behavioral context like foraging, our findings indicate that the stage
520 prior to nutritional independence, which is often defined as a sensitive period in a mammal's ontogeny
521 (Knudsen 2004; Walasek et al. 2014, 2022), also in meerkats is important towards their socio-ecological
522 development. Furthermore, the novel approach, disentangling dyadic affinity from general gregariousness,
523 allowed us to distinguish two sociality features that present an opportunity for greater comparability across

individuals, groups, and eventually species. Exploring sociality in using these two different features also allows for better understanding of social networks beyond the direct interactions occurring, and to consider indirect interactions, which have been suggested vital for animal societies (Brent 2015). As such, this study contributes to the understanding of developmental effects on mammal sociality and provides important insights into expanding methodological approaches in social network analysis towards disentangling the processes underpinning the dynamics of such systems.

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Supplementary Material

Table S1. Data collection summary.

Season	**Litter Name [Group]**	**Litter Size**	**Group Size Range**	**NN count** (incl. pups)	**NN count** (excl. pups)	**Group Focal Hours** (Total)	**Pup Focal Hours** (Total)
1	VAL2203 [AL]	3	11-17	813	1758	48.72	15.04
1	VL2203 [L]	4	22-29	1351	3562	39.1	24.09
1	VSI2301 [SI]	4*	11-15	1132	728	31.35	20.98
2	VDD2302 [DD]	4	10-15	287	0	20.14	20.14
2	VEC2302 [EC]	3	11-14	154	0	11.13	11.13
2	VUB2304 [UB]	4	16-18	220	0	17.74	17.74
2	VAL2303 [AL]	5	11-14	273	0	19.24	19.24
2	VJX2401 [JX]	4	15-19	245	0	19.14	19.14

Season refers to whether the litter was born, and therefore commenced study, between October 2022 – June 2023 (Season 1), or between October 2023 – June 2024 (Season 2). *NN count* refers to the number of individual Nearest Neighbour (NN) measures collected across scan sampling, either of pairs *including pups* or *excluding pups* (i.e. between other group members). For Season 1 litters, each group-wide scan would have as many NN measures as individuals present. For Season 2 litters, each scan had only the NN measure of the focal pup the scan was collected on. *Group Focal Hours* refers to the duration of focal follows conducted across all group members (including pups). *Pup Focal Hours* refers to the duration of focal follows conducted across the pups within each group across the full developmental period. *Avg. Pup Focal Hours* refers to the mean duration of focal follows per individual pup either at each *data week* during the developmental period, or across the full developmental period (*total*).

* At emergence, VSI2301 litter was confirmed as 5 pups, however only 4 survived to the first data week. Therefore, litter size was considered 4 for the purpose of this study.

Table S2. Focal data collection ethogram.

Behaviour	Definition
Scrabble	Scratches at the surface and moves whilst scratching at the ground, visually scanning the ground.
Forage	Actively digging in a single hole for prey for more than 2 seconds.
Re-forage	Returning to continue actively digging in the same foraging hole, or within 5cm.
Prey	Consuming of a prey item. Details entered include microhabitat, acquisition method, prey type, life stage of prey, prey state (dead/alive), processing of prey, prey size, count of items, and the outcome.
Pup-Fed (prey acquisition) / Pup-Feed (prey outcome)	A prey item provided by another individual. All prey details (above) given where known, as well as distance of the feeder, any avoided pups, and distance to the dominant female.
Following	An individual is tracking the movement of and following the direction of movement of another individual within 2 metres, making regular visual checks to their direction in the instance of any pauses in movement.

Partial ethogram of behaviours recorded during 20-minute focal follows. This ethogram only describes those directly of interest for this study. These definitions follow closely to those used across the long-term study as part of the Kalahari Meerkat Project protocols.

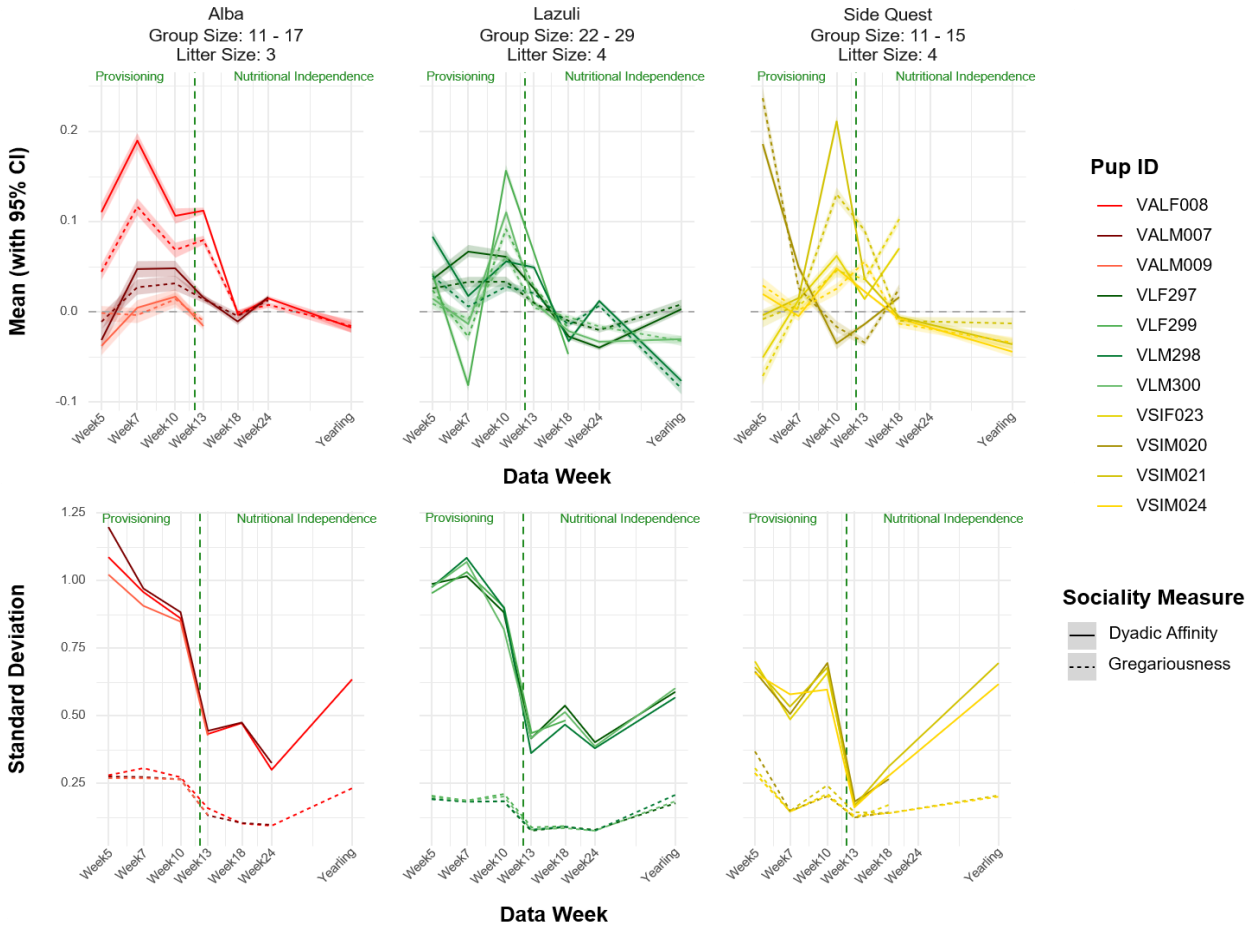

Figure S1. Longitudinal plots visualising the within- and between-group variation in the mean and standard deviation of dyadic affinity and gregariousness sociality values, for 11 pups, across 3 groups. Posterior values calculated by *bamoso* modelling of proximity social measures, and 95% confidence intervals surrounding the mean posterior values of dyadic affinity and gregariousness indicated with shading.

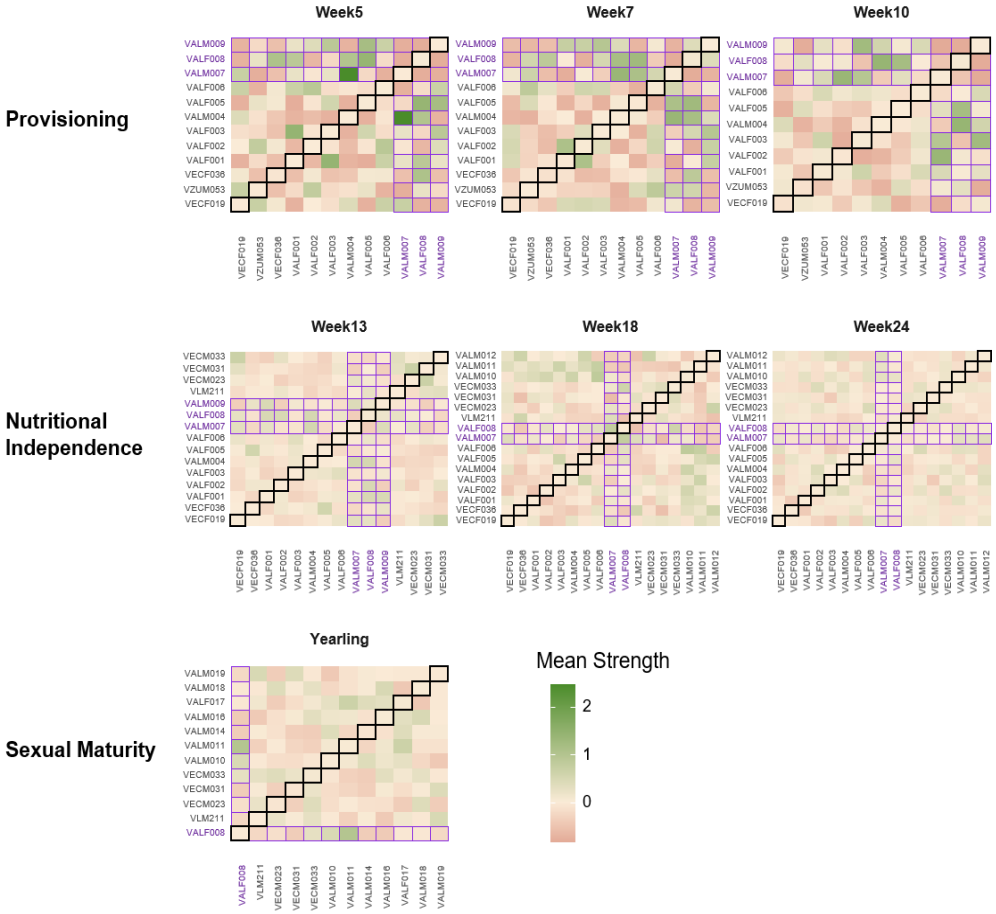

Figure S2. Heatmap of mean dyadic affinity and individual gregariousness values from 'Alba' across all data weeks. Each cell of the heatmap represents the mean strength of dyadic affinity between, or individual gregariousness of (central diagonal outlined in black), all group members of Alba across the studied data weeks. A value of 0 for both dyadic affinity and gregariousness is at the group mean. Focal individuals of interest of which the data week refers to their age are outlined in purple. Each row is split across three stages of development in regard to the focal individuals: period of provisioning as a pup, nutritional independence as a juvenile to subadult, and approximate sexual maturity at one year of age.

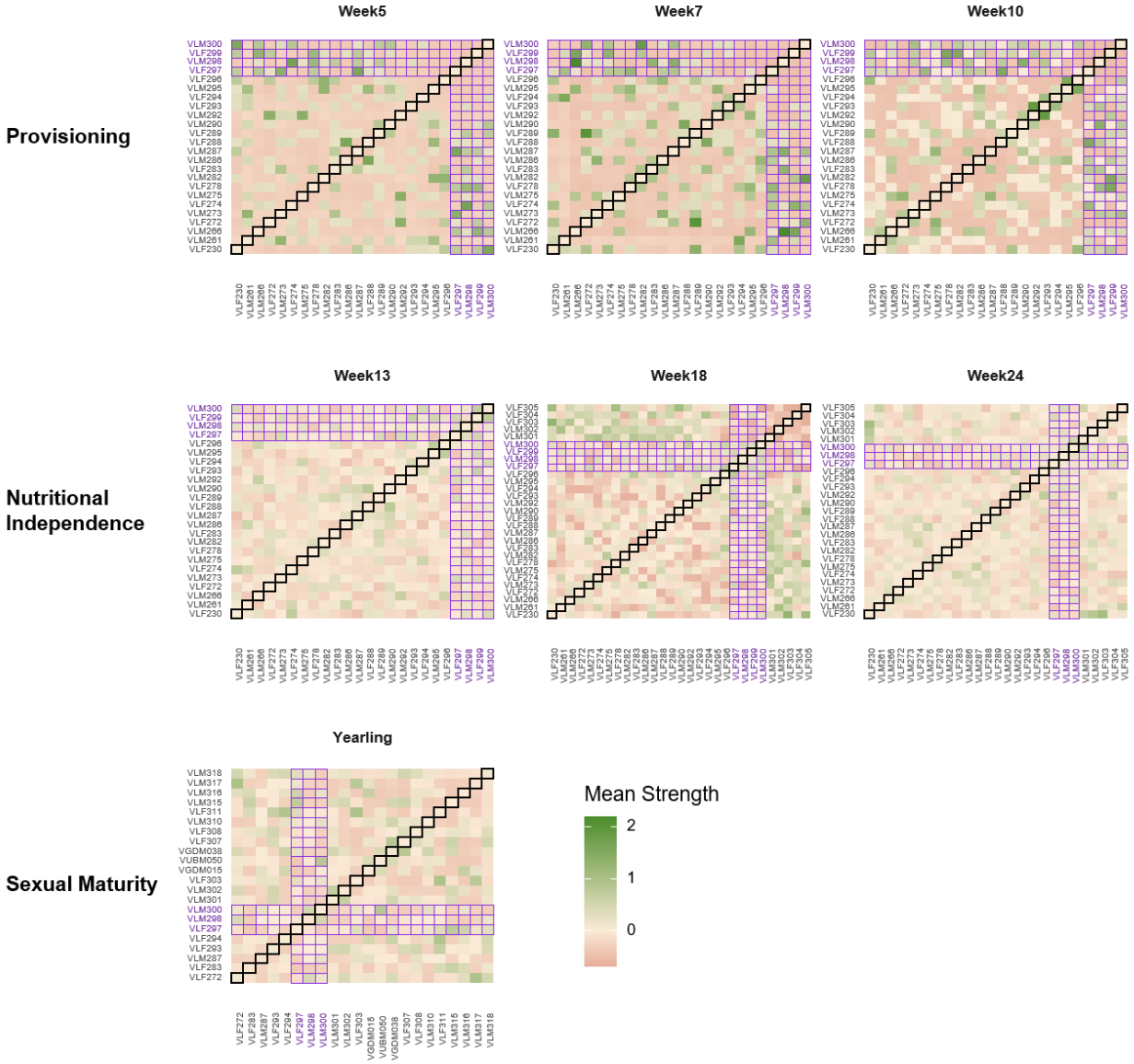

Figure S3. Heatmap of mean dyadic affinity and individual gregariousness values from ‘Lazuli’ across all data weeks. Each cell of the heatmap represents the mean strength of dyadic affinity between, or individual gregariousness of (central diagonal outlined in black), all group members of Lazuli across the studied data weeks. A value of 0 for both dyadic affinity and gregariousness is at the group mean. Focal individuals of interest of which the data week refers to their age are outlined in purple. Each row is split across three stages of development in regard to the focal individuals: period of provisioning as a pup, nutritional independence as a juvenile to subadult, and approximate sexual maturity at one year of age.

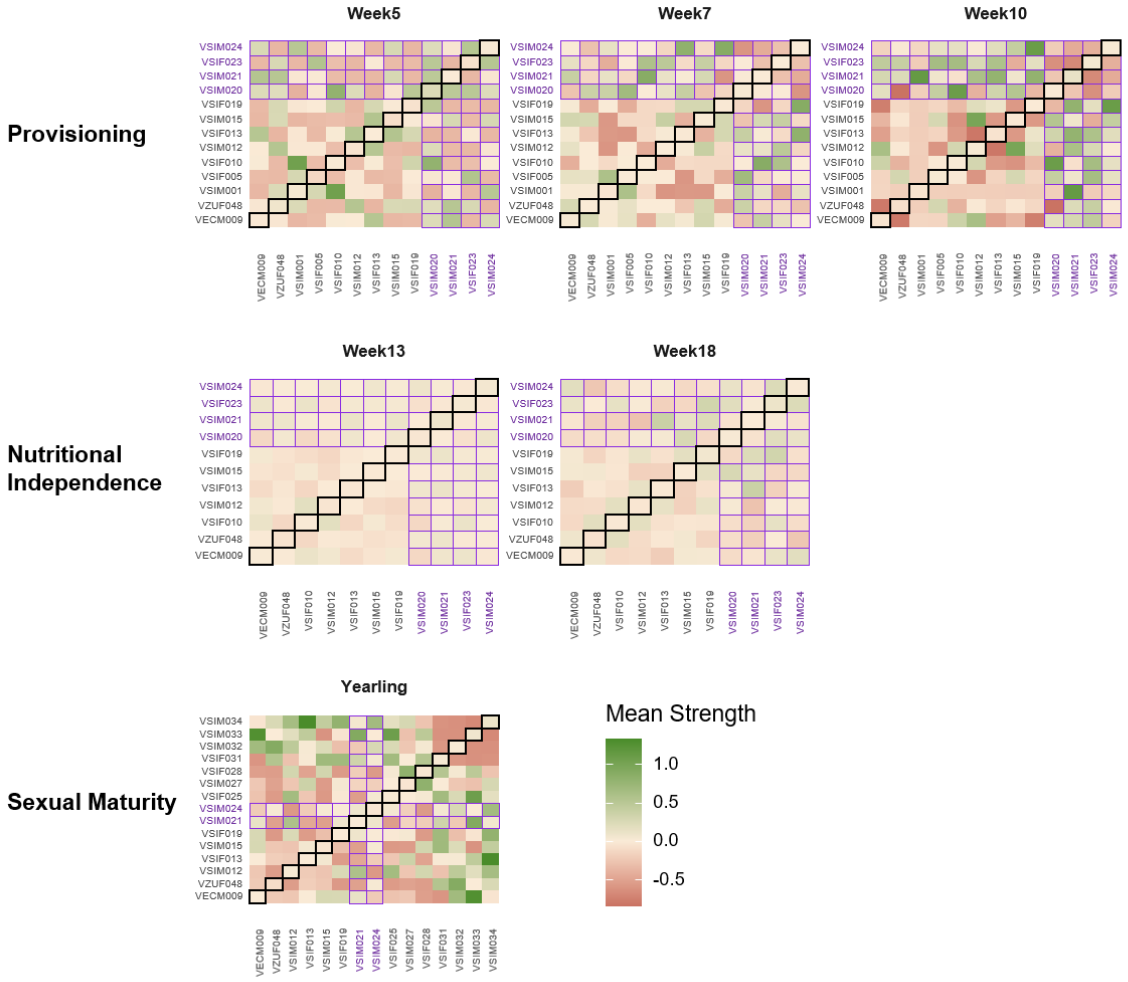

Figure S4. Heatmap of mean dyadic affinity and individual gregariousness values from 'Side Quest' across all data weeks. Each cell of the heatmap represents the mean strength of dyadic affinity between, or individual gregariousness of (central diagonal outlined in black), all group members of Side Quest across the studied data weeks. A value of 0 for both dyadic affinity and gregariousness is at the group mean. Focal individuals of interest of which the data week refers to their age are outlined in purple. Each row is split across three stages of development in regard to the focal individuals: period of provisioning as a pup, nutritional independence as a juvenile to subadult, and approximate sexual maturity at one year of age.