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

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Highlights

- We investigated two distinct sociality features: dyadic affinity and gregariousness
- Gregariousness remains stable with little variation across developmental time
- Dyadic affinity is heightened until the point of nutritional independence
- Nutritional needs during ontogeny drive short-term dyadic affinities in meerkats
- Both adult- and pup-initiated interactions influence short-term dyadic affinities

Abstract

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 have 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, Kalahari meerkats (*Suricata suricatta*). First, we describe within-group social dynamics during foraging with a focus on separating individual- from dyad-specific features. Second, we use these two sociality features to identify formation of social relationships during development. By combining proximity scans with data on social interactions from focal follows, we investigated the behaviours driving the observed social interactions. The strength of dyadic relationships between pups and adults was highest during pups' nutritional dependence and was positively linked to pup-care behaviours initiated by both adults and pups themselves. The strength of these dyadic relationships decreased 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 the ontogeny of social relationships in meerkats is shaped by the socio-ecology of cooperative pup care rather than a need for building long-term individualized relationships.

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

Introduction

Social species appear in a variety of dynamic systems reflecting adaptations to ecological pressures and behavioural plasticity (Alexander 1974; Ebensperger et al. 2012; Salguero-Gómez 2024; Ward and Webster 2016). Within species social traits and their links to fitness varies between individuals, depending on 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, within individuals, we have very limited knowledge of how social relationships fluctuate over time and how developmental trajectories determine an individual's social niche.

In competitive social species, groups are often composed of multiple-breeders, presenting a spectrum of hierarchies, multiple tiers, and fission-fusion dynamics (Clutton-Brock, 2016; Grueter et al., 2012; Ward & Webster, 2016; Wittemyer et al., 2005). In groups of such species, offspring can inherit social connections from their mothers or other similar vertical transmission of status through kin (Berman et al., 1997; East et al., 2009; Goldenberg et al., 2016; Ilany et al., 2021). Such social inheritance can benefit early-life survival (Silk et al., 2003; Turner et al., 2021; Zipple et al., 2021). In primates we know that throughout different life stages social selectivity can bring future beneficial relationships, such as avoiding costly competition and likelihood of disease contraction (Siracusa, Higham, et al., 2022; Siracusa, Negron-Del Valle, et al., 2022). In contrast, with limited evidence of long-term individualized relationships being present in cooperative breeding systems (Dunbar 1998; Salguero-Gómez 2024), these social species have been overlooked with regards to diversity of animal sociality. Studies investigating the formation of long-term bonds have focused on grooming and play networks, as these are expected to facilitate reciprocal sociality (Hodgson et al., 2024; Kutsukake & Clutton-Brock, 2010; Lazaro-Perea et al., 2004; Pellis et al., 2023). However, the behaviours that are important for social bonds likely differ between species and contexts. For example, in many social cooperative species, the foraging context (which take up large proportions of activity budgets) involves behaviours such as food 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).

Previous research have identified how stress during early in ontogeny can impact social positioning and therethrough later life reproductive success in brown-headed cowbirds (*Molothrus ater*) and zebra finches (*Taeniopygia guttata*) (Boogert et al., 2014; White et al., 2010). So far, the common method to assess social development has been cross-sectional comparisons between different groups, age classes, dominance statuses, or seasons (Barocas et al., 2011; Brent et al., 2013; Teunissen et al., 2018), or manipulations between a treatment and observational phase (Bentzur et al., 2021; Boogert et al., 2014, 2018; Brandl et al., 2021; White et al., 2010). Whilst these provide static snapshots covering variation across different life stages and begin to explore within individuals changes in sociality across life, they do not capture the mechanisms underlying how social relationships are formed and maintained. Longitudinal studies offer a stronger level of inference regarding the development of an individuals' social position and relationships over time (Brown 2017; Woodman et al. 2024). A longitudinal study of social networks during ontogeny in wild great tits (*Parus major*) identified a preference for fledglings to associate with siblings and peers as they started to become independent, whilst associating closer to adults by the timing of independence (Wild et al., 2024). Showing dynamic social strategies in a fast life history species with low parental care investment, this study highlights the importance of a longitudinal perspective considering critical periods of developmental change.

Furthermore, sociality entails variable components and distinguishing *dyadic affinity* (the propensity of two individuals interacting with one another specifically) from the individual level of *gregariousness* (the propensity of an individual to interact with any other conspecific) allows disentangling mechanisms underlying social interactions (Neumann & Fischer, 2023). It also creates a more fine-grained assessment of social structure, which is necessary to identify ecological relevance and changes in sociality over time (Neumann and Fischer 2023). For example, recently O'Hearn et al. (2024) showed that audience size around food owners was positively linked with the owner's individual gregariousness in Guinea baboons (*Papio papio*), whilst the identities of individuals with whom the owner shared food was explained by dyadic affinities between owner and audience members.

In this study, we expand this framework and use a longitudinal study design to examine social ontogeny and how developmental needs affects within-group sociality in a cooperatively breeding mongoose, meerkats (*Suricata suricatta*). In meerkats, within group social networks vary greatly between individuals and across different types of social interactions (grooming, dominance interactions, and foraging competition) (Madden et al. 2009, 2011) and do not reflect a consistent network (Gall and Manser 2018). Meerkat sociality also decreases in density when groups grow larger, possibly due to constraints in time budgets or socio-cognitive limitations in the number of connections that individuals can make and maintain (Madden et al. 2009). Thus far, developmental effects and offspring care have not been considered, both likely to be influential factors on within group sociality in species where cooperative care of young represents a key trait of their social system.

Repeated or extended interactions between two individuals are believed to be driven both by each individual’s own gregariousness, as well as their preference for one another over other individuals they may be able to associate with (i.e. within their group) (Neumann & Fischer, 2023). However, observing these directly and distinctly is not possible, and so disentangling and quantifying these sociality features from observable interactions is an important first step to exploring individual variation in sociality. We estimated *gregariousness* of individuals, and *dyadic affinity* (Neumann and Fischer 2023) from interaction and association data – to disentangle a) how meerkat pups develop their sociality during early life and b) how developmental needs impact the overall social characteristics of meerkat groups. 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). First, 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, we expected greater differentiation (i.e. large variation) in the dyadic affinities of pairs, which reflects the fluctuating within-group structure. In short, we expected to find smaller variance estimates for gregariousness compared to dyadic affinities.

Second, to describe early development in formation of social relationships, we investigated whether social bonds (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 natal burrow location to join the group while foraging, their social interactions would be highly dynamic and indiscriminate but become more selective towards cooperative adults as they age and can identify and act upon provisioning opportunities. Beyond the point of nutritional independence, we expected low variability in differentiated dyadic relationships due to the limited evidence of individualized social bonds in adult meerkats (Gall and Manser 2018; Madden et al. 2009, 2011).

Lastly, we aimed at identifying the biologically relevant behaviours that drive the social niche of meerkat pups. We asked whether pup-adult relationships during foraging are determined by adult-initiated food provisioning, 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, 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). If pups develop sufficient socio-cognitive skills to identify the adults that are most proficient food providers, one expects pups at this stage of ontogeny to benefit from positioning themselves near those adults that increase their likelihood of receiving provisioning. Consequently, we hypothesized that both adult-initiated provisioning and pup-initiated following interactions will positively link to spatial-temporal associations.

Methods

Study site & species

The study was conducted at the Kalahari Research Centre (KRC) in 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 fossilized dunes surrounding the dry riverbed of the Molopo River. Meerkats live in highly cohesive groups 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). Data collection covered two successive breeding seasons (Table 1): October 2022 to March 2023 (Season 1), and October 2023 to June 2024 (Season 2). We collected detailed focal follows (Altmann 1974) and spatial proximity scan data during foraging on total 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. Meerkat pups emerge from their birth burrow at 2-3 weeks of age, and this is when they are identified and marked. Pups remain in the close surroundings of their natal burrow until 3-4 weeks of age and are accompanied by one to multiple adult helpers, taking turns in guarding the pups at the burrow whilst the rest of the group forage (Clutton-Brock et al., 2001; Clutton-Brock & Manser, 2016). At approximately 4 weeks of age pups start to join the rest of the group to forage. Beyond lactational nutritional intake, pups are provisioned with prey captured by adults until approximately 12 weeks of age (Clutton-Brock et al., 2001). Around 12 weeks of age, pups reach nutritional independency but continue to hone their foraging skills beyond the provisioning stage until sexual maturity at 9-12 months of age (Duncan et al., 2025) and into adulthood (Jubber et al., 2025). To target the key points during development for each pup, we collected data at 7 time points across their first year of life, hereby referred to as data weeks (Figure 1).

We selected three data collection time points at 5-, 7-, and 10-weeks of age to capture potential fine-scale changes in sociality during this the initial and vital period of provisioning. To match the transition to foraging independence, we collected data at 13 weeks of age. We further covered the development of independent foraging skills until one year of age with three further data points: 18 weeks of age (mid-point of their juvenile stage), 24 weeks (transition into sub-adulthood and sexual maturity), and finally 1 year of age, when meerkats reach adult-level foraging efficiency (Duncan et al., 2025). Studied data weeks covered a short period before and after the relevant exact age. These periods were smaller at earlier weeks, to match the expected faster rates of developmental change, and larger at later weeks, when developmental change was expected to slow down. For data weeks 5 to 10, data within the 7 days prior and 6 days after reaching each age point were assigned to the relevant data week. For data weeks 13 to 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 to the pup's first birthday, and any data for the following year was considered for this data point. This ensured that for each individual, seven distinct time points of data were collected: three prior to nutritional independence, one at the point of reaching nutritional independence, and three subsequent across the remainder of the first year of life.

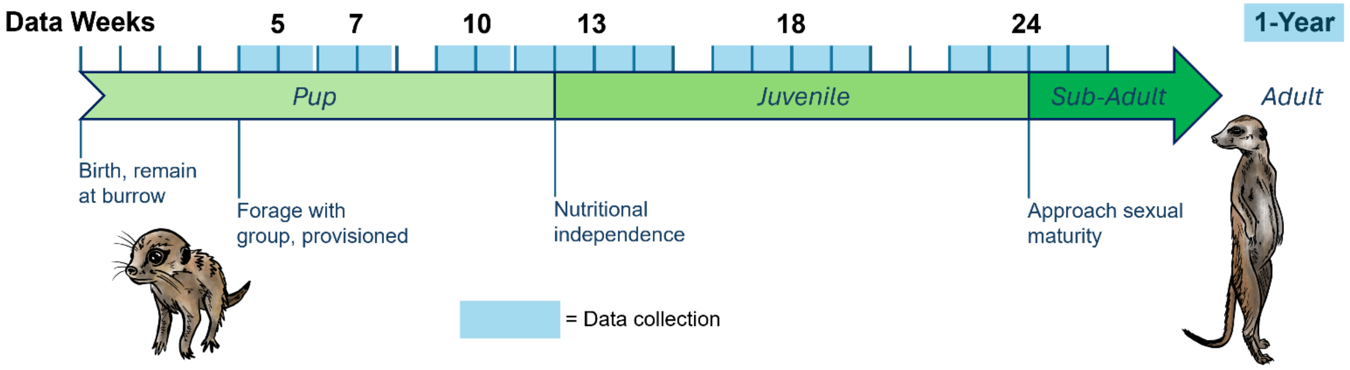

Figure 1: Timeline of meerkat pup ontogeny with major developmental transitions (noted in text). Numbers refer to the age (weeks), and therefore studied data weeks, with the blue highlights indicating the data collection period for each data week (see Methods). Meerkat illustration credit: Emily Stott.

Scan data collection

We collected spatial proximity data during foraging by noting the nearest neighbour identity and distance to the focal individual, with specific data collection protocols differing between the first and second breeding season. During the first breeding season we collected scan data on all individuals in the group by recording the identity of the closest group member (nearest neighbour) and their distance to our focal individual. For each scan, we aimed to collect all group member’s nearest neighbour in a randomised order based on sequential visual sight (average scan duration: 11.5 minutes, range: 2 – 46 minutes). Successive scans had a minimum of 20 minutes between collection. In total, with this protocol, we collected 571 group scans from 3 groups, with a total of 11 pups and 74 adults, at an average of 29 scans per group (and therefore per individual) per data week. Scan data from the first breeding season was used in all subsequent analyses. Due to time constraints on data collection, for the second breeding season we changed our protocol to what we refer to as ‘circle scans’. We collected proximity data (identity and distance) only for our study individuals (pups born in the season), and not for adults. However, we increased the level of detail of each proximity datapoint, by collecting the identity and distance of each group member within 10 meters of our study individuals. In total, we collected 1,179 circle scans across 5 groups, with a total of 20 pups and an average of 30 scans per pup per data week. The nearest neighbour data of these circle scans was used in our correlative analyses (see model 3) in addition to the nearest neighbour data of pups from the first breeding season. All scan sampling was conducted by trained researchers using Blackview BL8800 smartphones with a bespoke data collection form using Pendragon software (version 2.316A).

Focal data collection

We recorded all behaviours occurring during foraging by following each pup for an average of 0.92 hours per data week (range: 0.3 – 1.7). Where time permitted during both breeding seasons, we also followed a random subset of adult individuals for each study group for an aggregated average of 2.44 hours per data week (range: 0.33 – 6.4). This allowed for a greater observation effort of recording adult-to-pup interactions from the perspective of the adults. Individuals were closely followed by an observer between 1-2m in 20-minute bouts, during which all behaviours were recorded continuously by trained researchers. Similarly to scan data collection, data was collected using Blackview BL8800 smartphones with a bespoke data collection form using Pendragon software (version 2.316A). In total, this resulted in 210.2 hours of focal data collected on both pups and adults, across the 8 litters, 7 groups, and two breeding seasons. A detailed summary of data collected can be found in the supplementary materials, Table S1. An ethogram of the recorded behaviours can be found in the supplementary materials, Table S2.

Quantifying Sociality

For the aims of the study, we analysed three types of social behaviour during foraging contexts: *proximity* was the identity of the nearest neighbour individual (based on distance and collected from scan sampling, described above), *adult-initiated interactions* were considered as pup-feeding events where food is provisioned by an adult towards a pup or juvenile (collected from focal sampling, described above), 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; also collected via focal sampling).

Because the *proximity* data collected during the second season lacked a group-wide approach, our analyses focusing on the group-wide different measures of sociality (models 1-2), only included *proximity* data from the first breeding season (11 pups, from 3 groups, and 74 adults, see; Table S1: NN count including and excluding pups). For our analyses focusing on pup-centric perspectives of sociality (model 3), we used *proximity, pup-initiated* and *adult-initiated* interactions from both breeding seasons (31 pups, from 7 groups; Table S1: NN count including pups and total group focal hours across both breeding seasons). Importantly, though *proximity* data collection protocols differed between first and second season, we were able to account for these differences in our analyses for model 3 by focusing on only nearest neighbour measures that included pups from both breeding seasons, of which was consistently measured across both methodological approaches. See Table 1 for a simplified overview of the data collection and its application to the Methods and Results hereafter.

Table 1: Breakdown of data types and use in analyses as per Methods and Results.

Social Behaviour Type - Methodology	**Data Collection Period**	**Relevant Analyses** (see Methods & Results)
Proximity – Full Group Scans	Season 1 & Season 2	Models 1, 2, 3
Proximity – Pup-centric Circle Scans	Season 2	Model 3
Adult-initiated Interactions – Focal Follows	Season 1 & Season 2	Model 3

Pup-initiated Interactions – Focal Follows	Season 1 & Season 2	Model 3

Statistical analyses

Model 1. Calculation of sociality features

To calculate detailed sociality measures while accounting for confounding variables, we used a Bayesian modelling approach implemented in the '*bamoso*' R-package (Neumann and Fischer, 2023). This approach allows different behavioural data to be modelled jointly while accounting for relevant observation effort, and result in the calculation of both individual- and dyad-level sociality values. Within our model, we treated *proximity* and *adult-initiated interactions* as frequency of occurrence between all possible dyads, and *pup-initiated interactions* as the duration of time a focal pup followed another individual. For *proximity*, observation effort was calculated as the maximum number of instances each pair of individuals could have been recorded as nearest neighbours, based upon individual sightings within the groups at each data collection point. For both behavioural *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.

Our model then estimated two features of sociality, resting on the assumption that dyadic interactions and associations are driven by both *individual gregariousness* as well as *dyadic affinity* (Neumann and Fischer, 2023). 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). *b, gi,* and *rij* are estimated from the observed interactions *yij* and the observation effort E. For simplicity, we omitted the prior specifications from the equation. The model also 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 across our study population.

Model 2. Developmental changes of sociality: group-level measures

To compare the different sociality features across pups' developmental time with the measures retrieved from group members, we limited the behavioural data fitted within the *Bamoso* framework to the *proximity* data from the first breeding season (3 groups, 11 study subjects, 85 total individuals; Table S1, NN measures both including and excluding pups). Afterwards, we fitted two sets of multivariate Bayesian hierarchical models, one for each sociality measure (dyadic affinity and gregariousness).

For the analyses of the dyadic affinity values, we used as the response variable the dyadic affinity scores obtained from the posterior distribution of the model from the *Bamoso* framework. As predictors, we used developmental data weeks (as a scaled continuous time variable) and a binary explanatory variable of whether each dyad included a pup or not. We added an interaction term to assess any potential difference in longitudinal effect in relation to whether the dyad included a pup or not ("PairType"). To account for the potential effect of developmental time varying between individuals, we included random slopes for time for each individual. 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 our gregariousness analysis, we used as the response variable the mean gregariousness scores obtained from the posterior distribution of the model from the *Bamoso* framework. As predictors, we used the developmental data week (as a scaled continuous time variable), along with whether the individual was a pup or not ("IndividType"). Again, we accounted for the potential effect of developmental time varying between individuals, by fitting a random slope for time with the random effect of individual identification. Resultant formula = gregariousness ~ time * IndividType + (time || IndividCode). 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.

Model 3: Correlations among social behaviours

To assess whether any social behaviour (e.g. cooperative care) is correlated with another social assessment (e.g. proximity), an adaptation of our original model can allow for several observed interaction types to be modelled together, and correlation coefficients among the underlying affinity and gregariousness features to be estimated as follows (example with two behaviours):

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

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

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

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

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

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

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

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

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

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

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 behavioural interaction or proximity types, while simultaneously estimating the correlation coefficients. In other words, for two behaviours y and w, we estimated 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.

Therefore, to identify links between the different sociality measures (*proximity, pup-initiated* and *adult-initiated interactions*), we fitted scan and focal follow data from both breeding seasons (Table S1: NN measures (incl. pups) only, and Group Focal Hours; Total dyads considered: n = 489) to this framework, and extracted correlation coefficients between measures for both gregariousness and dyadic affinity. These analyses were based on the comparison of pups' social measures, with matrices centred around the interactions that included minimum one pup without considering adult-adult interactions. We analysed three pairwise correlations between different affiliative behavioural matrices generated from the models. Pup-initiated matrices explored correlations between *proximity* and *pup-initiated* following interactions. Adult-initiated matrices explored correlations between *proximity* and *adult-initiated* pup-feed interactions. Pup-care matrices explored the correlations between *pup-initiated* following and *adult-initiated* pup-feed interactions. It should be noted that because the frequency of pup-care behaviours decrease after nutritional independence (12 weeks of age), and in situations when a new litter is born into the group (i.e. younger pups were present resulting in focal individuals contributing to the care of younger pups rather than receiving pup-feeds), we only looked at correlation coefficients of these interactions up to week 13. This way we ensured a suitable sample size of data, whilst avoiding incorrect interpretation of interactions related to pup care of litters not included as study subjects.

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

Ethical Note

All data was 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), and 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).

Results

Model 1. Calculation of sociality features

To first disentangle the general structure of group sociality, we explored dyadic affinity and gregariousness of all group members and possible dyads from the proximity data of the first breeding season. 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). Thus, dyadic affinities show more differentiated values than individual gregariousness. 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, our data also indicate that individual variation exists as to the actual mean values of dyadic affinity and gregariousness, both within- and between-groups (Figure S1).

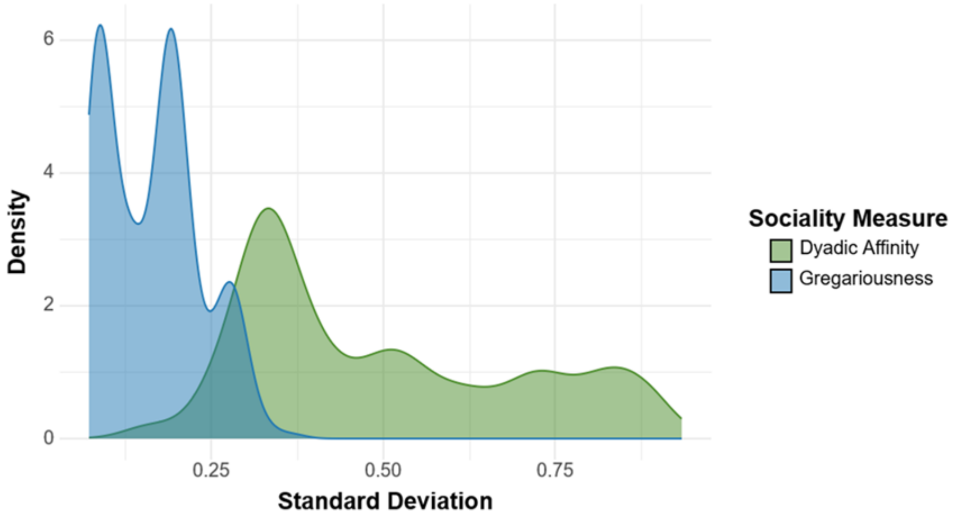

Figure 2. Density plot of standard deviation values of gregariousness and dyadic affinity of all individuals and dyads. Calculated by *bamoso* modelling of proximity social measures, aggregated for the entire study period. The densities represent aggregated posterior distributions over time points and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

Model 2. Developmental changes of sociality: group-level measures

Having established the different sociality features, we then explored how dyadic-affinity and gregariousness may change over ontogeny, considering a pup’s sociality within its group. The following results present proximity data from the first breeding season only, with the purpose to distinguish between dyadic-affinity and gregariousness, and further to evaluate whether such pup-adult relationships are maintained over time.

Affinity

We found that dyadic affinity changed temporally across early development (Figure 3.A, model outputs are in Table 2), and that this pattern differed between pair types. Average dyadic affinities decreased over developmental weeks for pairs which included pups (purple line in Figure 3.A), whilst slightly increasing over time for pairs without pups (orange line in Figure 3.A). At the youngest data time point, i.e., shortly after pups emerge from the burrow and start foraging, average affinities were higher in pairs with pups compared to pairs without pups, and this pattern was reversed once pups reached sub-adulthood and sexual maturity.

Table 2: Model outputs for affinity.

	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

Gregariousness

We did not observe any notable temporal changes or differences between pups and adults in their average gregariousness (Figure 3.B, Table 3), i.e., gregariousness showed stability over time and similar values in pups and other group members.

Table 3: Model outputs for gregariousness.

	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

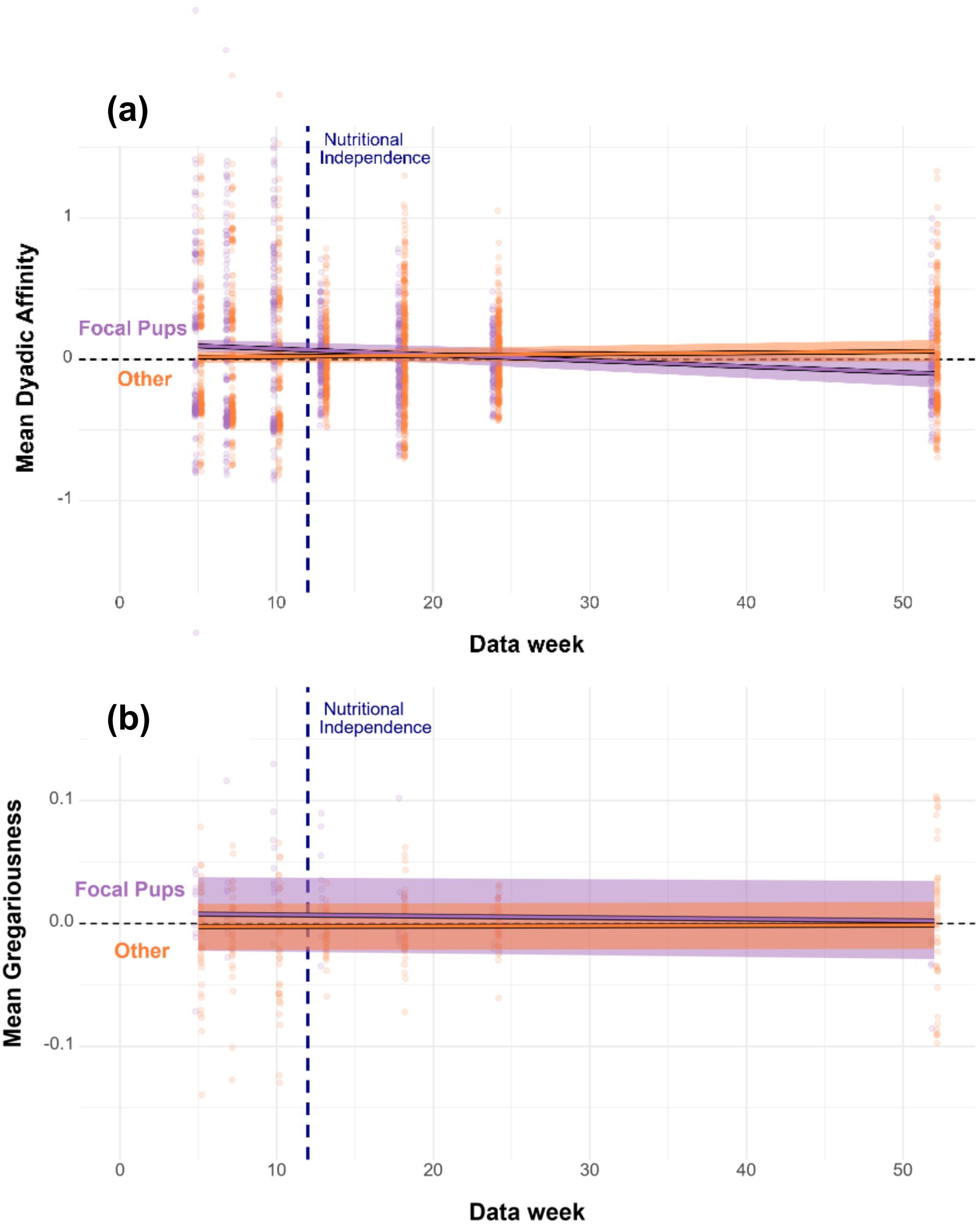

Figure 3. Temporal variation in (a) dyadic affinity and (b) gregariousness values between pups and other group members. 'Focal Pups' refers to the focal individuals that were pups at the start of the study, with the data weeks therefore referring to their developmental age. 'Other' includes all older 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 around the median (central linear trend line). Individual posterior means are represented by the individual data points. Data covers 85 individuals - 11 of which are focal pups - and all possible dyads from the 3 groups the focal pups were born into.

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. These 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 (adult stage) (Figure 4).

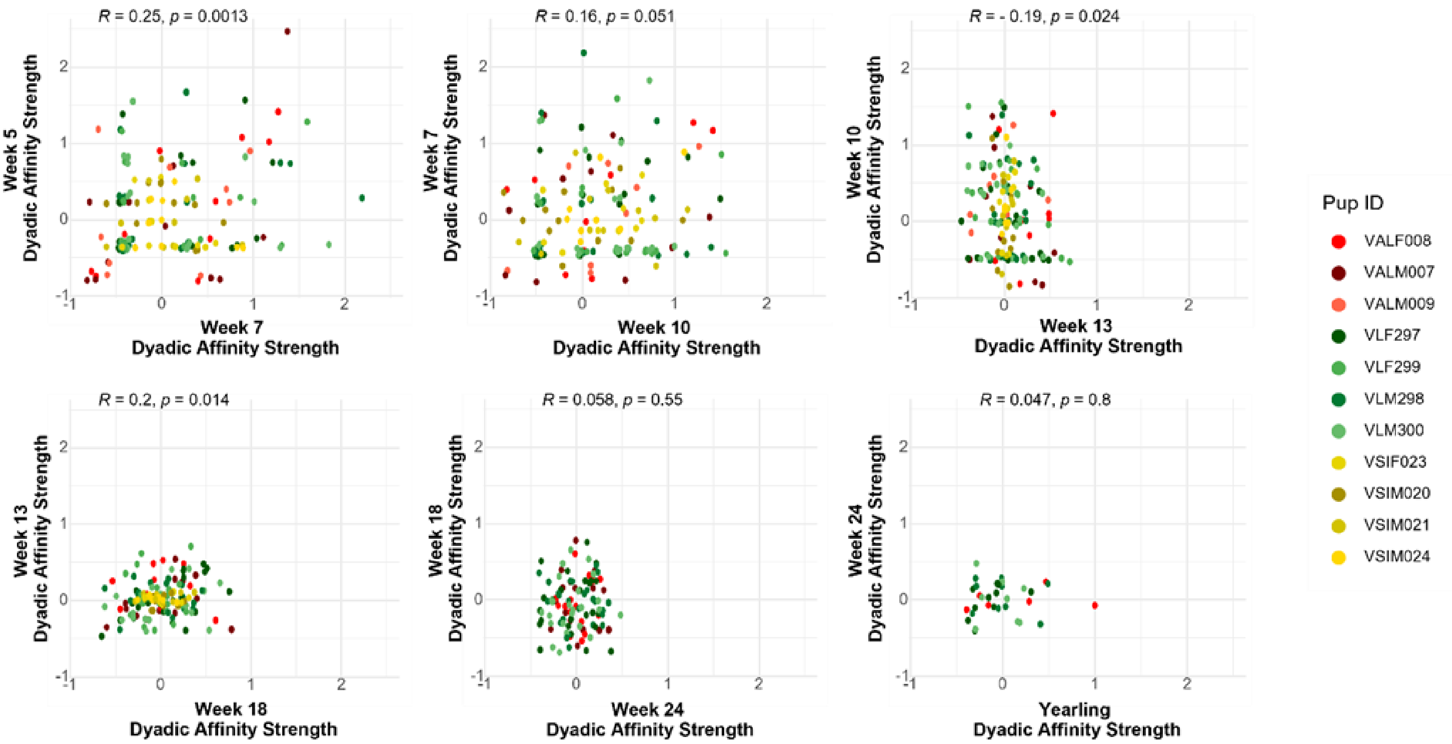

Figure 4. Pearson's correlation coefficients of the strength of dyadic affinity values of pup-adult dyads between consecutive data weeks of 11 pups across the studied period, where specific dyadic pairings are present in both consecutive weeks. Identification of the pup included in the dyads identified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

Model 3. Correlations among social behaviours

Using the established features of sociality, we then evaluated to what extent pup-initiated and adult-initiated pup-care behaviours predict pups' spatial proximity within their groups. Due to the pup-centric perspective, we included data from both breeding seasons, and combined pup nearest neighbour proximity scan data with observed pup-adult interactions from focal follow data.

Our data showed small positive correlations between dyadic affinities for all three pairs of behaviours prior to nutritional independence (most posterior medians ~ 0.2, Figure 5). After the point of nutritional independence, these relationships 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). Also, these estimates were associated with large uncertainties.

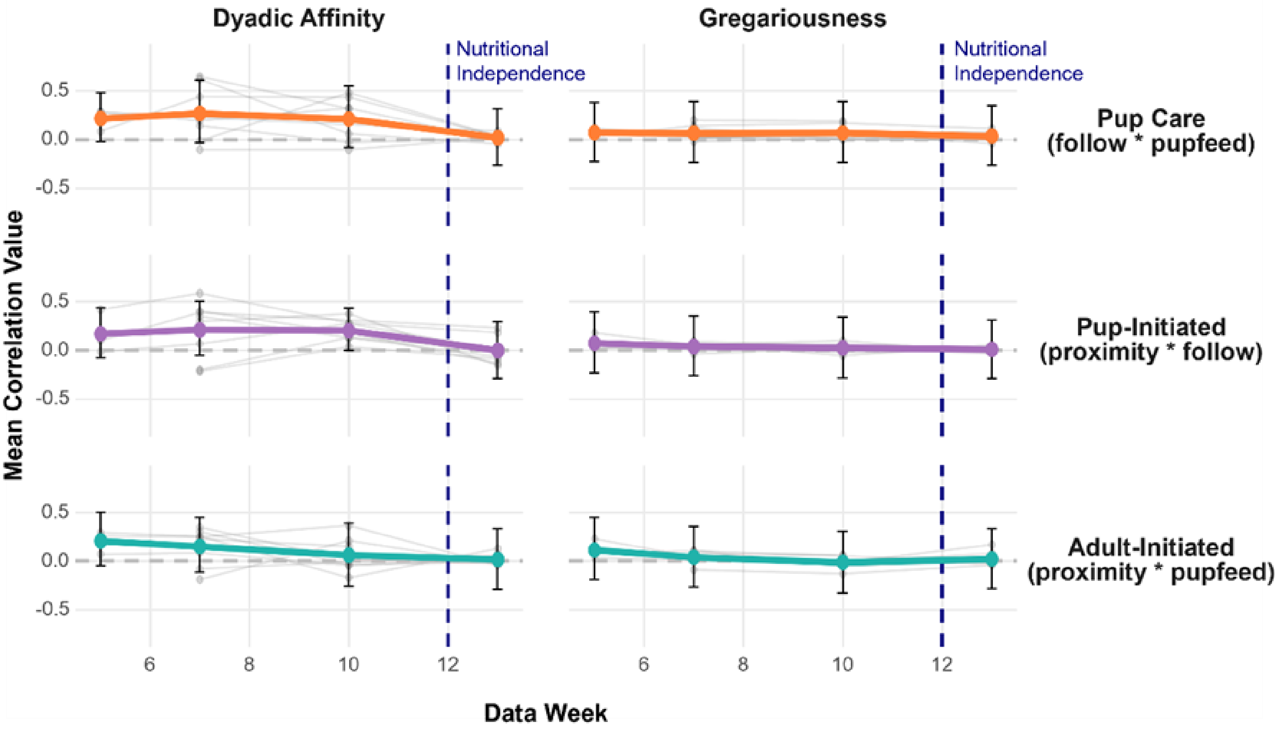

Figure 5. The change in correlation coefficients between sociality measures (dyadic affinity and gregariousness) generated from different behavioural interactions. The mean correlation value indicates the strength of the correlation from posterior correlation coefficients generated with *bamoso* models. Coloured points and lines represent the overall mean posterior value for each behavioural 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

We studied developmental trajectories of meerkat sociality during foraging by adopting a recent 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). First, disentangling two distinct features of sociality, we found that social dynamics of meerkat groups are better described by variation in dyadic relationships, rather than by individual differences in their gregariousness (Figures 2 & 3). Second, we found that dyadic relationships formed between pups and adults were strongest prior to nutritional dependence, and decreased thereafter, whilst gregariousness showed no such temporal change over the time span investigated. Finally, we combined observational and proximity data to assess whether social interactions during development were driven by the species cooperative pup-care. Here, we found modest correlations between pup-care behaviours, including both adult and pup-initiated provisioning interactions.

We showed that dyadic relationships during foraging are foremost formed between pups and adults in the breeding time when meerkat groups raise offspring. Gregariousness, on the other hand remain low and stable across individuals and time. Cohesive decisions in meerkats, such as movement speed and direction, are determined through quorums with no clear initiator (Bousquet et al. 2011). Considering this, our findings align with the expectation that maintaining a similar level of gregariousness across the entire group, that is stable propensities to interact with any individual within the group, can facilitate the success of such quorums and help meerkats maintain their high cohesiveness necessary for their cooperative social system. Since meerkats show high within-group relatedness (Griffin et al. 2003), we expect there are limited genetic confounding factors on the within-group social structure. It is plausible that the observed low variability in gregariousness is reinforced by the 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 such as dyadic-affinity and gregariousness, could be critical when considering demographic factors, such as relatedness, across taxa, and enable greater comparability.

After establishing the distinct sociality features within meerkat groups, we explored how both dyadic affinity and gregariousness change over early development. In particular, we examined the greater variation found in dyadic affinities, and whether this variation was driven by the nutritional needs of developing pups. We identified that when meerkat groups have pups present, dyads including pups declined in their affinity over developmental time, showing heightened dyadic affinity strength prior to 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. For meerkats, dyadic relationships are most important during early ontogeny when relationships between pups and adults are critical for survival, as these social interactions ensure pups with sufficient food provisioning and simultaneously provide critical learning opportunities necessary to acquire foraging independence. Diet learning in meerkats is facilitated by adults "teaching behaviour" altered over ontogeny as pup begging calls change when they grow (Thornton, 2008b, 2008a). Our behavioural data describing pups following adults, though preliminary, further indicate that the pups themselves also are attentive towards provisioning adults (Figure 5).

The dyad-level affinities correlated positively only up until nutritional independence but not thereafter. Pup-initiated following interactions maintained a weak positive correlation for a longer period past nutritional dependence compared to adult-initiated pup-feed interactions, which approached zero prior to nutritional independence when pups were 10 weeks old, (Figure 5). Despite that all these estimates showed considerable uncertainty and hence must be taken as preliminary, it provides an initiative to further explore whether pups play a greater role in driving proximal associations than adults as their social skills mature.

Moreover, the trends of dyadic affinity strength (Figure 3.A.) prior to nutritional independence could also 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 to maximize growth and/ or skill development. Meerkats reach adult-level asymptotes of foraging skills only at the timing of their sexual maturity and morphological asymptotes of growth, suggesting physiological constraints on foraging ability up until 9-12 months of age (Duncan et al., 2025). As such, it is possible that there is a conflict of interest between pups and adults regarding provisioning amounts.

While studies on adult sociality in meerkats have resulted in no specified individual relationships, we here explored whether any shorter-term evidence of such was present during the early developmental period. From calculating correlation coefficients of dyadic affinity strength between pups and adults across consecutive developmental weeks, we found small positive correlations between the strength of specific dyadic relationships prior to 10 weeks of age, when relationship strength of pups and adults peaked. Thereafter, these factors correlated negatively across the timing of nutritional independence at approximately 12 weeks of age (Figure 4) before levelling off at correlations of around 0. Overall, this suggests that any specification of relationships between individual meerkats is restricted to early development, and there is no maintenance of such bonds beyond this period.

Conclusions

We conclude that meerkat foraging sociality is driven by their dyadic affinities, rather than general gregariousness. Our results show that the strengthened dyadic relationships during the critical developmental period of nutritional dependency, relate to the socio-ecological needs of cooperative pup care, necessary for survival and diet learning in meerkats with limited need for long-term individualized bonds.

Zooming into a typically less-social behavioural context like foraging, our findings indicate that the stage prior to nutritional independence, which is often defined as a sensitive period in a mammal's ontogeny (Knudsen 2004; Walasek et al. 2014, 2022), in meerkats is important towards their socio-ecological development. Furthermore, by disentangling dyadic affinity from general gregariousness, we were able to disentangle two sociality features. This presents an opportunity for greater comparability across individuals, groups, and eventually species, thereby allowing for a 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, focusing on a highly cooperative system, this study contributes to the understanding of developmental effects on mammal sociality and provides insights into expanding methodological approaches in social network analysis towards disentangling the processes underpinning the dynamics of different social systems.

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Declaration of Interest:

None

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

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	29.48†	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	23.07	23.07
2	VEC2302 [EC]	3	11-14	154	0	19.15	19.15
2	VUB2304 [UB]	4	16-18	220	0	24.14	24.14
2	VAL2303 [AL]	5	11-14	273	0	19.24†	19.24
2	VJX2401 [JX]	4	15-19	245	0	24.63	24.63

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.

† All focal hours of litter VAL2303 overlap with the 1-year data week period of VAL2203. Therefore, the total focal hours considered for VAL2203 would be 48.72 with the 19.24 from VAL2303 inclusive. These were excluded in the VAL2203 table count to not incorrectly inflate the actual total focal hours of 210.2.

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.

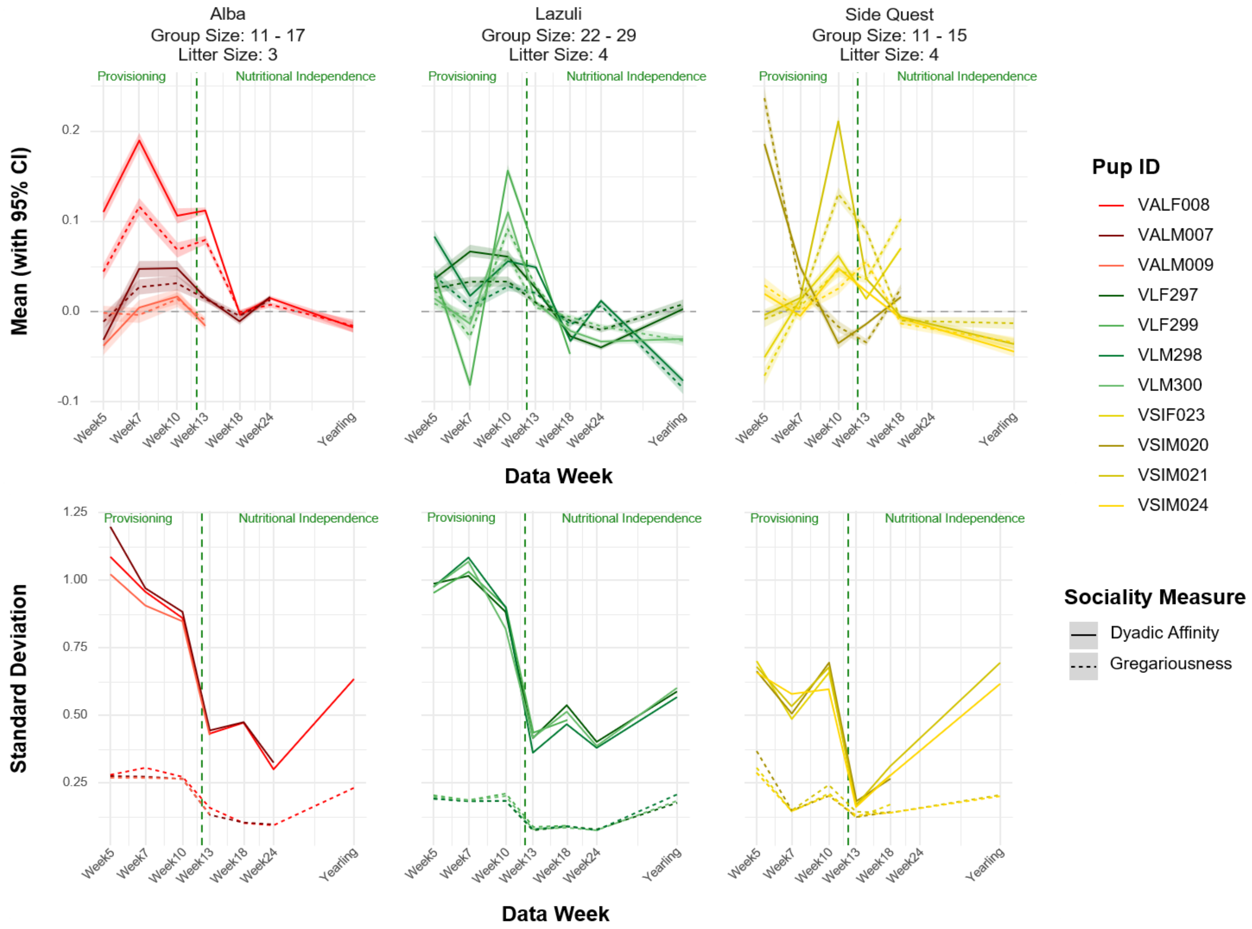

Figure S1. Longitudinal plots visualising the within- and between-group variation in the mean and standard deviation of dyadic affinity and gregariousness sociality values, for 11 pups, across 3 groups. Posterior values calculated by *bamoso* modelling of proximity social measures, and 95% confidence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

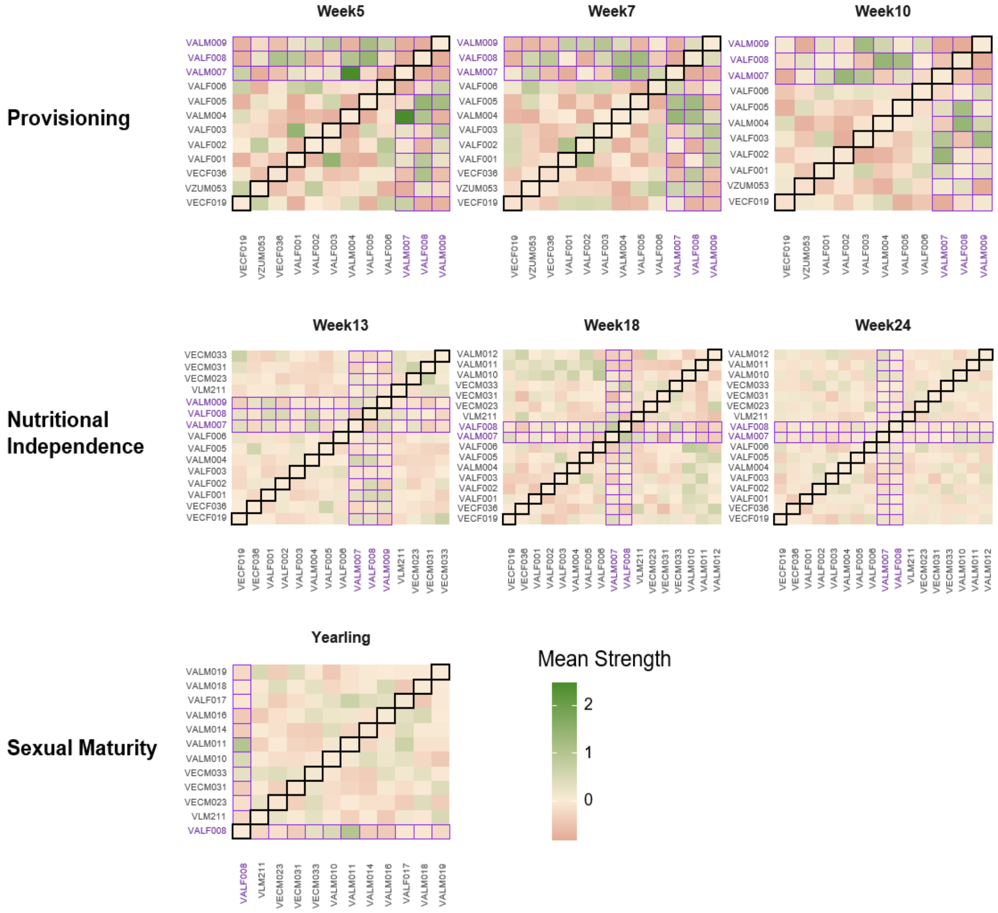

Figure S2. Heatmap of mean dyadic affinity and individual gregariousness values from 'Alba' across all data weeks. Each cell of the heatmap represents the mean strength of dyadic affinity between, or individual gregariousness of (central diagonal outlined in black), all group members of Alba across the 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.

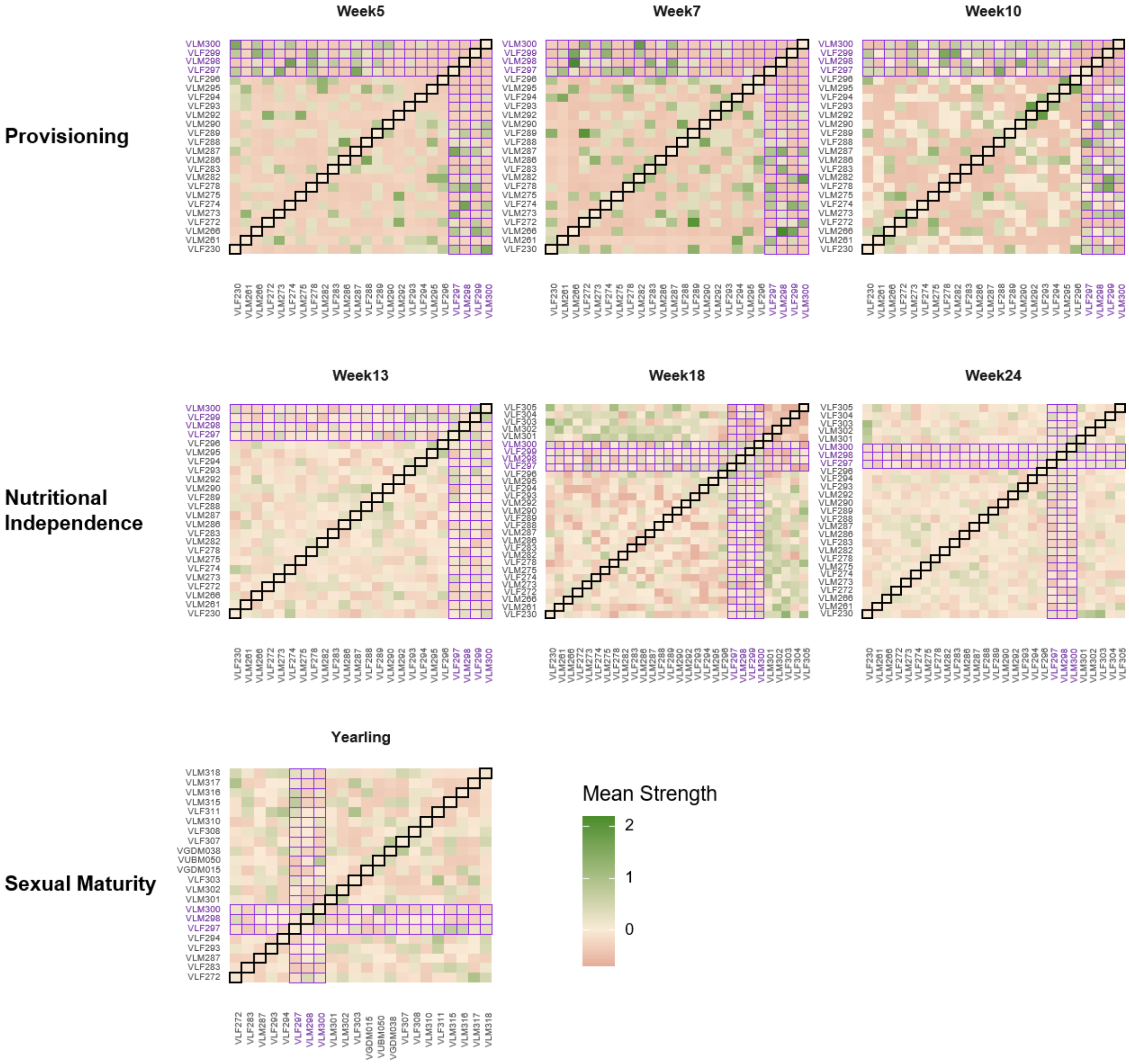

Figure S3. Heatmap of mean dyadic affinity and individual gregariousness values from ‘Lazuli’ across all data weeks. Each cell of the heatmap represents the mean strength of dyadic affinity between, or individual gregariousness of (central diagonal outlined in black), all group members of Lazuli across 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.

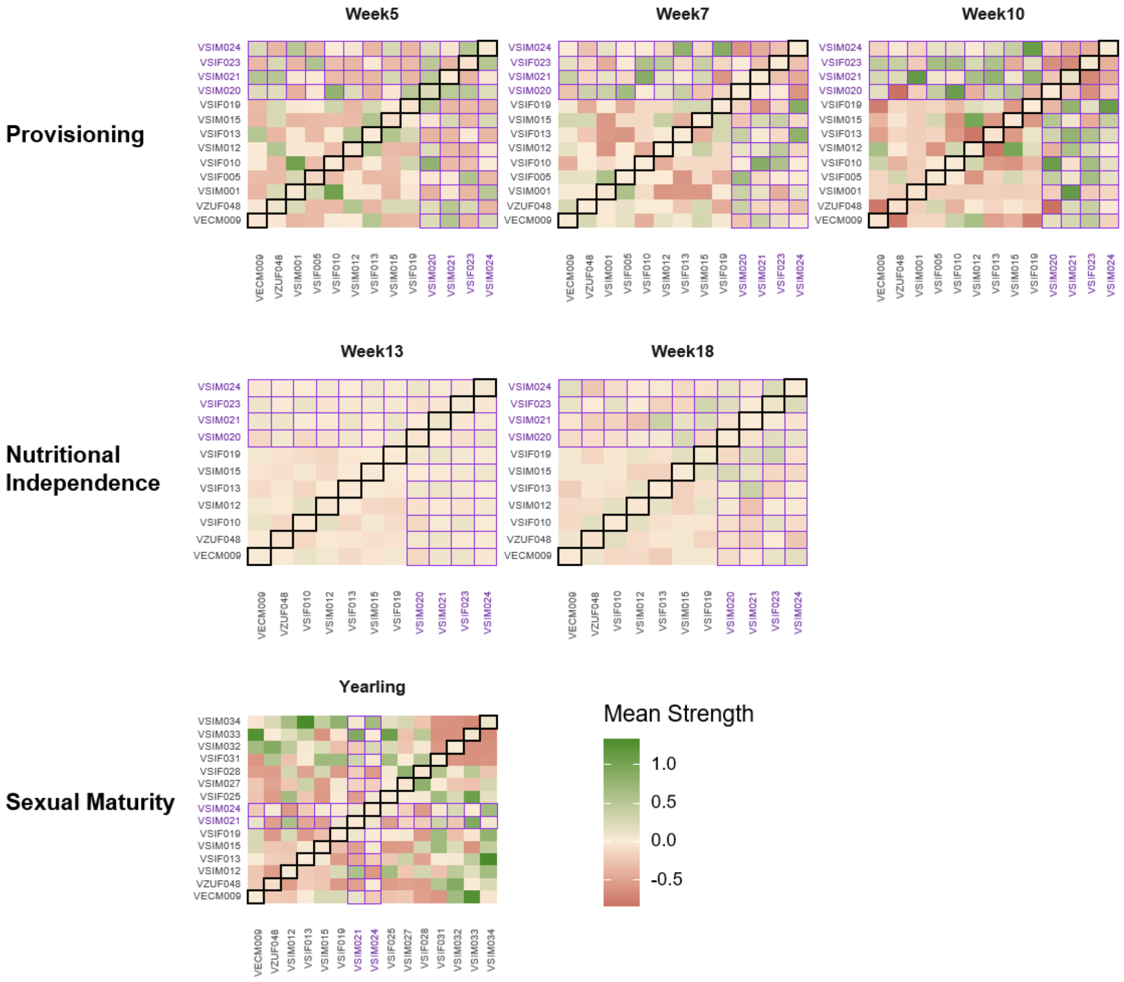

Figure S4. Heatmap of mean dyadic affinity and individual gregariousness values from 'Side Quest' across all data weeks. Each cell of the heatmap represents the mean strength of dyadic affinity between, or individual gregariousness of (central diagonal outlined in black), all group members of Side Quest 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.