Title: Contributions of genetic and non-genetic sources to variation in cooperative behaviour in a cooperative mammal.

Running title: Genetics of cooperative behaviour

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Acknowledgements

Data accessibility

Data and code for reproducing the main analyses are available through the Dryad Digital Repository database (https://doi.org/10.5061/dryad.cfxpnvx68). The data and code for the meta-analysis of heritability estimates of selected traits in wild mammals is available in Supporting Information (Files S3-S5).

Conflict of interest statement

The authors declare no conflict of interest.

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Abstract

The evolution of cooperative behaviour is a major area of research among evolutionary biologists and behavioural ecologists, yet there are few estimates of its heritability or of its evolutionary potential and long-term studies of identifiable individuals are required to disentangle genetic and non-genetic components of cooperative behaviour. Here we use long-term data on over 1800 individually recognisable wild meerkats (*Suricata suricatta*) collected over 30 years and a multi-generational genetic pedigree to partition phenotypic variation in three cooperative behaviours (babysitting, pup feeding and sentinel behaviour) into individual, additive genetic and other sources, and to assess their repeatability and heritability. In addition to strong effects of sex, age and dominance status, we found significant repeatability in individual contributions to all three types of cooperative behaviour both within and across breeding seasons. Like most other studies of the heritability of social behaviour, we found that the heritability of cooperative behaviour was low. However, our analysis suggests that a substantial component of the repeatable individual differences in cooperative behaviour that we observed was a consequence of additive genetic variation. Our results consequently indicate that cooperative behaviour can respond to selection, and suggest scope for further exploration of the genetic basis of social behaviour.

Key words: quantitative genetics, heritability, cooperation, cooperative breeders, animal model

Introduction

In species with cooperative and eusocial breeding systems, some adults forego breeding and assist others in protecting and feeding their offspring (e.g., Cant, 2012). The evolution of

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such behaviours, where an individual's actions benefit others and involve some fitness costs to themselves, is of particular interest because the traditional theory of natural selection is based on competition among individuals (Clutton-Brock, 2009). In the early 1960s W. D. Hamilton published a series of papers on this topic (Hamilton, 1964a, 1964b, 1963). They led to the development of a number of approaches for modelling social evolution, including kin and levels-of-selection models as well as quantitative genetic formulations of Hamilton's rule (Bijma and Wade, 2008; McGlothlin et al., 2014). However, despite a large volume of literature on the evolution and distribution of cooperation and substantial evidence of pronounced individual differences in cooperative behaviour, there have been few quantitative estimates of the repeatability or heritability of individual differences and we know little about the relative contributions of genetic differences and variation in the social and non-social environment (Kasper et al., 2017b).

Here, we describe evidence of heritable variation in cooperative behaviour in wild meerkats (*Suricata suricatta*) from the Kalahari. Unlike eusocial societies, where workers are sterile and individuals follow divergent developmental pathways that determine the role that they will play within the colony (Boomsma and Gawne, 2018; Crespi and Yanega, 1995), all individuals in cooperative vertebrates are potential breeders. Subordinate individuals may either disperse to breed, compete for the breeding position in their natal group, or remain as non-breeders that queue for the breeding position (Clutton-Brock, 2016). If they take the last of these courses, they may either assist the breeding female in raising her young or may conserve their resources for their own.

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Among non-breeding subordinates that elect to stay and assist dominant breeders, there is variation both in the form and degree of help that they provide (Bergmüller and Taborsky, 2010; Clutton-Brock et al., 2001a, 2001b, 2000; Duncan et al., 2019). The contributions of helpers to cooperative activities are typically conditional on their sex, age, weight, condition and recent foraging success (Clutton-Brock et al., 2001a, 2002; Cockburn, 1998; Gilchrist and Russell, 2007; Russell et al., 2003a; Wright et al., 2001). In addition, they are likely to be affected by social interactions with other group members. The effect of the 'social environment' here includes variation in the needs of juveniles and the number of helpers that can contribute to satisfying them (Adams et al., 2015; Brotherton et al., 2001; Clutton-Brock et al., 2003; Rotics and Clutton-Brock, 2021; Russell et al., 2003a), with the result that individual contributions to cooperative activities vary considerably with the group's size and age/sex composition, and the ratio of helpers to dependent juveniles.

Individuals may also differ consistently in their contributions to cooperative activities after the usual effects of age, sex and group size have been allowed for (Bergmüller et al., 2010). The use of mixed-effects models for the partitioning of phenotypic variance have made it possible to measure the repeatability of these differences (e.g., Dingemanse and Dochtermann, 2013), and have shown that, after the effects of age, sex and group size have been allowed for, there exist repeatable differences in cooperative behaviour between individuals in long-tailed tits (*Aegithalos caudatus;* Adams et al., 2015), banded mongooses (*Mungos mungo*; Sanderson et al., 2015), and Damaraland mole-rats (*Fukomys damarensis*; Thorley et al., 2018).

The existence of individual variation in a trait means it can be subject to selection, but for an evolutionary response to occur this variation must have an underlying heritable

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component. Analyses of parental behaviour show that a significant proportion of individual variation in contributions to offspring care is the result of interactions between environmental and genetic factors that affect the development of individuals and that these differences can be partly heritable (e.g., Dor and Lotem, 2010; Freeman-Gallant and Rothstein, 1999; MacColl and Hatchwell, 2003; Schroeder et al., 2019; Wetzel et al., 2015). As yet, only a few studies of cooperative behaviour have been in a position to explore the extent to which individual differences in cooperative behaviour are heritable. For example, a study of western bluebirds (*Sialia mexicana*), where analysis is based on a seven-generation pedigree, showed that a strong genetic component underlies the propensity to help rather than to breed and that the probability of having a helper at the nest is also partly heritable (Charmantier et al 2007). In addition, a study of wild long-tailed tits (*A. caudatus*) used long-term individual-based data to show that individuals differed consistently in cooperative activities and that there was evidence of genetic variance in juvenile provisioning (Adams et al., 2015). A recent study of banded mongooses (*M. mungo*) used a double pedigree approach with the 'natural cross fostering' occurring in this species to tease apart genetic and social inheritance in the propensity and amount of babysitting and pup escorting performed by each sex, finding additive genetic variance in male propensities only (Nichols et al., 2021). Laboratory studies of cooperatively breeding cichlids (*N. pulcher*) have also used careful breeding designs, standardised environments and controlled behavioural tests to separate genetic from non-genetic sources of (co)variation in helping and other social behaviours, finding that helping behaviour is partly heritable in this species – although differences among individuals are driven primarily by non-genetic factors, including maternal effects and effects of the permanent environment of individuals rather than by additive genetic effects (Kasper et al., 2019, 2017a).

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These few studies highlight the need for repeated observations of individuals across time and social contexts in order to determine the extent to which individual differences in cooperative behaviour are heritable and have the capacity to evolve. If not accounted for, whether statistically or via sampling or experimental design, such sources of individual or shared variation may be apportioned incorrectly. For example, a study of Kalahari meerkats (*S. suricatta*) found relatively high levels of repeatability in cooperative behaviours, but did not control for factors such as the size or identity of the group (English et al., 2010). If differences among groups (due to, for example, group size or membership) are relatively stable, this source of shared within-group variation might inflate estimates of individual differences. Furthermore, investigating the role of the social environment is particularly important for studies of cooperative behaviour precisely because such behaviours involve interactions with other individuals (Kasper et al., 2017b), which can have consequences for the total heritable variation available to selection and for the evolutionary dynamics of the behaviour (McGlothlin et al., 2010; Moore et al., 1997).

Here we use data from our long-term study of a wild population of meerkats (*S. suricatta*) to investigate the relative contributions of genetic and non-genetic sources to observed variation in three different forms of helping behaviour ('babysitting', 'pup feeding', and 'sentinel behaviour'). Meerkats are cooperatively breeding mongooses living in groups of up to 50 individuals, with a dominant pair monopolising reproduction and subordinates of both sexes assisting in rearing young (Clutton-Brock et al., 2001a). Females can produce up to 4 litters per year, with litter sizes ranging from 1-7 pups (Clutton-Brock and Manser, 2016). Helpers are typically animals of both sexes of between 6 months and 4 years of age that have remained in their birth groups, though some groups also include one or more subordinate

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immigrant males, who also contribute to cooperative activities (Clutton-Brock et al., 2001a, 2001b). All group members contribute to a range of cooperative behaviours including 'babysitting' and 'pup feeding' as well as 'sentinel behaviour', though the breeding pair rarely contribute to babysitting (Clutton-Brock et al., 2004; Clutton-Brock and Manser, 2016). Babysitting entails one or more individuals remaining with the pups at the natal burrow to protect them against potential predators or neighbouring groups for up to 10 hours a day without feeding while the rest of the group leaves on their daily foraging trip (pup ages 0-20 days). Pup feeding involves helpers and parents finding and giving food items to pups when they are old enough to join the foraging group but are unable to forage independently and so beg for items from adults (20-90 days). Sentinel behaviour occurs during foraging trips and entails an individual ceasing foraging and climbing to an elevated position to scan the area, from which it will give distinct calls on a regular basis to enable other individuals to reduce their own vigilance behaviour as well as alarm calls to warn the group if it detects a predator (Clutton-Brock et al., 1999; Manser, 1999).

The contributions of individuals to all three cooperative acts vary with their age, sex and breeding status: dominant breeders tend to contribute less than non-breeding subordinates, and females contribute more than males to babysitting and pup feeding and less to sentinel behaviour (Clutton-Brock et al., 2004, 2003, 2002; Duncan et al., 2019). Helping contributions vary with the helper's age and condition (Clutton-Brock et al., 2002; Russell et al., 2003b), and the decision over whether to feed a captured prey item to a pup or eat it themselves varies with the pup's hunger and associated begging level (Russell et al., 2002). A previous study of the same population of meerkats found consistent differences among individuals in both babysitting and pup feeding contributions, although there was no further investigation of

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the source(s) of the repeatable component (English et al., 2010). Our analysis also includes sentinel behaviour, where group members alternate in keeping guard from a raised position while the group is foraging by digging in the ground (Clutton-Brock et al., 1999; Santema and Clutton-Brock, 2013). Both non-breeding subordinates and dominant breeders contribute to acting as sentinels when the group is foraging, and – like contributions to other cooperative activities – individual contributions to sentinel behaviour also vary with factors including age, sex and weight (Clutton-Brock et al., 1999). Meerkats appear to be 'indiscriminate altruists', and there is currently no evidence that variation in their contributions to cooperative activities is related to their relatedness to the current litter or the group they are in (Duncan et al., 2019).

We used detailed information on individuals, groups, and genetic relatedness between individuals to assess the contributions of genetic and non-genetic sources of variation in three cooperative behaviours. For each behaviour in turn, we investigated the average effects of various aspects of the focal individual (including age, sex and social status), in addition to measurable differences between litters and groups. We used 'animal models' (Wilson et al., 2009) to disentangle effects of: (i) additive genetic variation; (ii) non-genetic short-term individual variation (variation among individuals over multiple observations within a single breeding season); (iii) non-additive genetic long-term individual variation ('permanent environment', or variation among individuals over all observations, which also includes non-additive genetic effects); (iv) maternal effects (genetic and environmental); (v) shared litter effects (i.e., similarities between littermates caused by their shared early life environment); (vi) the shared environment within groups (which includes social effects) at different timescales (i.e., average differences among groups across observation periods, breeding season, and over the entire dataset); and (vii) breeding seasons. We provide estimates of both short- and long-

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term repeatability (i.e., measures of stable individual differences) and the heritability for each behaviour. We also test whether there is evidence for genotype-by-age interactions in each behaviour, which might indicate genetic variation for behavioural trajectories over ontogeny.

Methods

Groups and life histories

Meerkat groups typically include a dominant breeding pair that virtually monopolise reproduction, with subordinate individuals of both sexes helping to protect and feed juveniles born into the group (Clutton-Brock and Manser, 2016). The dominant female is usually either a founding member or was born in the group and is responsible for most breeding attempts. Dominant females usually breed 2 – 4 times per year and can maintain their position for over ten years, producing more than 80 pups over their lifetime, although reproductive output typically peaks at around five years of age (Thorley et al., 2020). One dominant male (usually an immigrant) guards the dominant female and fathers most of her offspring (>80%; Spong et al., 2008). Dominant males may hold their tenures until their own death or that of their partner, but face strong competition from mature immigrants or members of other groups and so usually have a shorter tenure relative to dominant females (Clutton-Brock et al., 2006a). Subordinate females typically remain in their natal group for 2 – 3 years and contribute to cooperative activities. Around the age of two, subordinate females also begin attempting to breed occasionally, though their breeding attempts commonly fail (Clutton-Brock et al., 2001b). However, older subordinate females become targets of increased aggression from the dominant female, with over 90% leaving before they are 4 years old; all subordinate females are ultimately driven out of the group unless they acquire dominant status (Clutton-Brock et al., 2010, 2006b; Kutsukake and Clutton-Brock, 2006). Subordinate males also contribute to

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cooperative activities within their natal group, but begin 'roving' (leaving the group for a day at a time) at around 2 years old. Subordinate males rarely breed in their natal group, but occasionally do with subordinate females in other groups (Spong et al., 2008); dispersal is therefore necessary for acquiring a dominant breeding position. Natal males will eventually fail to return to their natal group due to having joined another established group, formed a new one, or been killed.

Our study is based on data collected on over 60 groups of meerkats in a population in the southern Kalahari Desert, South Africa. In any given year, the number of groups habituated to human observers varied from 5-24 and the higher total number of groups in our sample reflects the fact that groups commonly died out as a result of variation in breeding success and survival (Clutton-Brock and Manser, 2016). All individuals in our study groups were habituated to observation from within a metre or two, with animals tagged with transponder chips and individually recognizable by dye marks on their fur. In any year, we were usually able to monitor the contributions of all group members to all three cooperative activities in all breeding attempts per year (usually 2 or 3) in 5 – 15 groups of habituated animals and to weigh individuals regularly by enticing them to climb onto electronic balances in the field. Groups were visited several times a week by teams of observers who monitored variation in individual contributions to three main cooperative activities (Clutton-Brock et al., 2003, 2002). Observers were moved among groups to average out any potential observer bias effects.

Cooperative behaviour

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We calculated measures of pup feeding and babysitting on a per-litter basis, with observations spread across litters reared in up to 46 different breeding groups where almost all individuals were recognizable and had been monitored since their birth. We measured individual contributions to babysitting as the number of half days an individual remained to babysit a litter of pups in the period from the birth of the litter until the pups start foraging with the rest of the group (n = 6,989 observations on 1,645 individuals over 545 litters across 46 groups, ranging from 1-30 observations per individual, mean observations per individual = 4.3). Babysitting is measured on a half-day basis as a change in babysitter can occur if groups return to the sleeping burrow in the middle of the day. We measured individual contributions to pup and juvenile feeding as the number of occasions an individual meerkat was observed to bring food to a begging pup during the peak period of provisioning (30-75 days) (Brotherton et al., 2001) (n = 6,509 observations on 1,539 individuals over 507 litters across 40 groups, ranging from 1-30 observations per individual, mean observations per individual = 4.2). We measured individual contributions to sentinel behaviour as the duration of time (in minutes) spent as a 'raised guard' during foraging trips. As this behaviour is observed on all foraging trips, we group measurements into 3-month 'bins' (Duncan et al., 2019), starting when the focal individual is 3 months old (n = 12,333 observations on 1,776 individuals across 40 groups, ranging from 1-45 observations per individual, mean observations per individual = 6.9). For each behaviour, over 60% of individuals were observed over multiple breeding seasons, and over 60% of individuals were observed multiple times within each breeding season. For both pup feeding and sentinel behaviour, we also use the total observation time of the group to control for variation in observation period (see statistical analysis below).

Pedigree details and construction

We constructed a multigenerational pedigree by identifying the parents of each individual in the population (Kruuk, 2004; Pemberton, 2008). Establishing and validating parentage in wild populations can be error-prone (particularly for paternity) if based only on observational data and we consequently used genetic analysis of 18 microsatellites derived from small tissue samples from individuals' tail tips (collected over 19 years, 1998-2017) supplemented with observational field data (female pregnancies and male distributions in space and time) for error correction and to add maternity where genetic data were missing (Griffin et al., 2001; Nielsen et al., 2012). Parentage and sibship inference was performed using COLONY2 (Wang, 2004; Wang and Santure, 2009) and MASTERBAYES (Hadfield et al., 2006); the resulting multigenerational pedigree was prepared in the R package pedantics (Morrissey et al., 2007) for use in the analyses, and to determine inbreeding coefficients for each individual. Full details of pedigree construction are provided by Nielsen et al (2012). The final pedigree included 3539 individual records with 3167 maternal and 2345 paternal links (from 304 distinct dams and 318 distinct sires respectively), with a maximum depth of 10 generations.

Statistical analysis

We analysed all data using the 'animal model' approach (Wilson et al., 2009) in generalised linear mixed effects models using the MCMCglmm package (Hadfield, 2010) in R version 3.6.1 (R Core Team, 2019) with the multigenerational pedigree as described above. Babysitting was fitted as a logistic regression of the number of half-days babysitting ('successes') vs the difference between the maximum possible number of half-days and the number of half-days spent babysitting ('failures'). Pup feeding was fitted with an overdispersed Poisson model for count data, and the number of minutes that the group was observed over the

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entire period (natural log-transformed) was included as a covariate to account for observer effort. Sentinel behaviour was also fitted with an overdispersed Poisson model, and the number of observation minutes (natural log-transformed) included as a covariate. Further details of fixed and random effects are given below. We used weakly informative parameter-expanded priors for the random effects (V = 1, nu = 1, alpha.mu = 0, alpha.V = 25^2). We ran all models for 510 000 iterations, removed the first 10 000 iterations to ensure stable convergence of model chains, and sampled every 50th iteration (resulting in a final chain length of 10 000). We evaluated convergence through visual checks of the chains, the Heidelberger diagnostic, and checking that autocorrelation between successive samples of the MCMC chain was below 0.1. We checked that models were robust to different prior distributions (see Supporting Information File S1 for details) and ran each model several times to ensure that the chains were converging to similar results. We report coefficients for fixed and random effects (and derived estimates such as heritabilities) as posterior means with 95% highest posterior density (HPD) credible intervals (CrIs) unless otherwise stated.

We included a set of standard fixed effects for models of each behaviour (babysitting, pup feeding, sentinel behaviour). Group size (mean-centred) was included in all models. We followed English et al. (2010) by fitting distinct age categories ('sub-adult', 0-12 months; 'yearling', 12-24 months; 'adult', 24+ months), and extended this by also modelling a continuous age effect (in months, centred at 24 months) that was allowed to vary across categories (i.e., an interaction between age category and continuous age in months) to model non-linearity in age-related variation. We also included the individual's sex, dominance status, and the interaction between these variables. The focal individual's inbreeding coefficient (as estimated through the pedigree structure) was included as a covariate, mean-centred and standardised to 1 standard

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deviation units (SDUs). Maternal weight at the focal individual's birth was also included, mean-centred and standardised to 1SDU, to model any direct maternal effect (if maternal weight was unavailable it was set to the mean value, i.e. 0). For babysitting and pup provisioning models only, we also included whether the litter being cared for was born in the wet (October-April) or dry (May-September) season. We also included the sequence that litters are born to a breeding female within each breeding season (breeders can have up to 4 litters within each July-June breeding season) in these models. Fixed effects are considered statistically significant if the 95% HPD CrIs exclude zero, and we also report Markov Chain Monte Carlo p-values (pMCMC; the probability that the posterior distribution includes zero).

For each model, we included a range of random effects to partition phenotypic variance: pedigree identity (additive genetic variance); focal individual's litter identity (shared effects among littermates); individual-within-breeding season (short-term individual variation); focal individual identity or 'permanent environment' (permanent individual variation); maternal identity and maternal pedigree identity (maternal environment and maternal genetic effects); group at observation period (shared current environment: per-litter for babysitting and pup feeding, per-3 month bin for sentinel behaviour); group within breeding season (shared short-term environment); group identity (shared long-term environment); and breeding season. For the sentinel behaviour model, we also included an effect of the month that the 3-month observation period started. We cannot use the same criteria to assess 'significance' for random effects as for fixed effects (i.e., that the 95% CrIs exclude 0), because random effect variance components are constrained to be non-negative and thus their 95% CrIs will always exclude 0. Visual inspection of posterior modes is the most suitable option to check whether the posterior distribution is strongly clustered at 0, and we use a heuristic to assess the relative 'importance'

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of a random effect term to improving model fit. A posterior mode in the lowest 25% quartile of the range indicates limited support for a given random term explaining non-zero variance.

Each behaviour required the use of non-Gaussian error distributions for modelling, thus we use the R package QGglmm (de Villemereuil et al., 2016) to estimate repeatabilities and heritabilities on the observed data scale for pup feeding and sentinel behaviour and on the liability scale for babysitting (de Villemereuil et al., 2013). These methods are necessary for the correct interpretation of evolutionary potential. We calculate the individual repeatability as the contribution of additive genetic, maternal, focal litter (shared early life environment) and the individual permanent environment effects to overall phenotypic variation. These are sources of variance that contribute to stable individual differences. We also calculate short-term individual repeatability as above but with individual-within-breeding season added to the numerator. Heritability is calculated as the contribution of additive genetic variance V_A to overall phenotypic variation V_P. We use the QGLMM package to estimate the contribution of fixed effects variance and include this in V_P when calculating repeatability and heritability estimates.

Finally, we extended the models for each behaviour to test for age-related genetic variation in two ways. First, we allowed the pedigree and permanent environment identities (additive genetic and individual differences) to vary (linearly) with age by fitting random slopes to these model terms. We also allowed residual variance to differ across the three age categories. Second, we fit models where all terms that contribute to stable individual differences (additive genetic, maternal, focal litter, and permanent environment) were allowed to vary – and co-vary – across the three age categories. Again, we also allowed residual variance to differ across the three age categories. We report full details of fixed and random effects from all

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models in Tables S1-S9 in Supporting Information File S2. The data and R code needed to replicate these analyses, along with pre-compiled versions of the models described above, are available on Dryad (Houslay et al. 2021).

Results

Babysitting

Individual contributions to babysitting increase at a high rate during the first year of life, continue to increase over the second year (albeit at a lower rate), and then slowly decrease over later life until individuals leave their birth group between the age of three and four years (Figure 1B, Table S1). Across all ages, males are less likely to babysit pups than are females. Dominant breeders are less likely to perform babysitting duties than subordinates (dominant = -2.63, 95% CrI = (-2.83, -2.43)), although this effect is less pronounced in male dominant breeders (male × dominant = 0.73, 95% CrI = (0.49, 0.97)). In large groups – where the ratio of helper to pups is relatively high – individual contributions to babysitting by individual are reduced (Figure 1C; group size = -0.06, 95% CrI = (-0.07, -0.06)). Individual contributions to babysitting increase with litter size (litter size = 0.06, 95% CrI = (0.03, 0.09)). There is no significant interaction between these parameters (group size × litter size = -0.000, 95% CrI = (-0.003, 0.004)). Individuals that are more related to the litter tend to babysit less (average relatedness of focal to litter = -0.31, 95% CrI = (-0.53, -0.08)).

There is low long-term repeatability of babysitting ($R_{long-term}$ = 0.08, 95% CrI = (0.06, 0.09)), but individuals are slightly more repeatable within seasons ($R_{short-term}$ = 0.12, 95% CrI = (0.11, 0.13)). These estimates include important contributions both of additive genetic and of

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early life effects (Figure 2A). The heritability of babysitting is relatively low (h^2_{liab} = 0.05, 95%

CrI = (0.03, 0.07) ; Table 1). We found no indication that age trajectories in contributions to

baby-sitting vary between individuals or that there are genetic differences in these trajectories

(variance in slopes not distinct from 0 in both cases; Table S2). Genetic variances show some

differences across age categories but with strongly overlapping credible intervals in addition to

very high positive cross-age correlations (Table 2A; Table S3). Shared litter effects are strongest

at the sub-adult stage and not significantly different from zero thereafter, while residual

variation increases from lowest at the sub-adult stage through to highest as adult.

Pup feeding

Individual contributions to pup feeding vary with age, peaking within the first 2 years

and subsequently decreasing throughout later life as the age of dispersal approaches (Figure 1E;

Table S4). Across all ages, males feed pups on average less often than do females, and dominant

breeders feed pups less often than do non-breeding subordinates (dominant breeders = -0.24,

95% CrI = (-0.35, -0.13)). The frequency of pup feeding by a given individual declines in larger

groups where helper:pup ratios are high (Figure 1F; group size = -0.07, 95% CrI = (-0.08, -

0.06)), and increases in larger litters (litter size = 0.08, 95% CrI = (0.04, 0.12)). There is no

significant interaction between these parameters (group size × litter size = -0.005, 95% CrI = (-

0.011, 0.001)). Individuals that are more related to the litter tend to contribute more to pup

feeding (average relatedness of focal to litter = 0.51, 95% CrI = (0.35, 0.69)).

The long-term repeatability of pup feeding is low ($R_{long-term}$ = 0.10, 95% CrI = (0.07,

0.13)), and the small individual-within-breeding season effect leads to only a minor increase in

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short-term repeatability (Figure 2B; $R_{short-term}$ = 0.12, 95% CrI = (0.09, 0.15)). Much of the observed variance is explained by the shared current environment, which indicates that there are differences in average provisioning (over the entire group) to any given litter. The repeatable variation we found is explained largely by additive genetic and shared litter effects rather than maternal and/or permanent environment effects. The heritability of pup feeding is significant but is once again low (h^2_{obs} = 0.05, 95% CrI = (0.03, 0.08) ; Table 1). There was no evidence for age-related trajectories in contributions to pup feeding at either the individual or genetic level (variance in slopes not distinct from 0 in both cases; Table S5). When allowing genetic effects to vary across age categories, we found that these are similar and strongly correlated (cross-age category correlation estimates ranging from 0.93 to 0.95; Table 2B; Table S6). However, we found that residual variation increases from lowest at sub-adult stage to highest as adult. Shared litter effects are strongest early in life, declining thereafter, but are low relative to residual variation (especially at the adult stage), such that – while the expression of genetic variation may be relatively stable – the heritability of pup feeding declines with age.

Sentinel behaviour

Time spent on sentinel behaviour increases rapidly during the first year of life and moderately over the second year, decreasing thereafter (Figure 1H; Table S7). Males spend more time on sentinel behaviour than do females (male = 0.69, 95% CrI = (0.51, 0.88)). Female dominant breeders engage in this behaviour less than do non-breeding subordinates (dominant = -0.32, 95% CrI = (-0.52, -0.11)), but dominant breeding males spend more time on sentinel behaviour relative to non-breeding subordinate males (dominant × male = 0.85, 95% CrI = (0.57, 1.13)). Individuals in larger groups spend less time on sentinel behaviour (Figure 1I; group size = -0.05, 95% CrI = (-0.06, -0.05)). We also found a positive effect of maternal weight

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on time spent on sentinel behaviour, suggesting a direct maternal effect on this behaviour (maternal weight = 0.11, 95% CrI = (0.00, 0.20)).

Repeatability for sentinel behaviour is low, both at long- and short-term ($R_{long-term}$ = 0.03, 95% CrI = (0.02, 0.04); $R_{short-term}$ = 0.03, 95% CrI = (0.02, 0.05)). The small amount of repeatable variation is driven largely by significant additive genetic and shared litter effects (Figure 2C). The heritability estimate for sentinel behaviour is very low (h^2_{obs} = 0.01, 95% CrI = (0.01, 0.02); Table 1). There was no evidence for either individual or genetic age-related trajectories (variance in slopes not distinct from 0 in both cases; Table S8). Across age categories, genetic variances are similar (Table 2C; Table S9) and strongly positively correlated. Shared litter effects are strongest at the sub-adult stage and decline thereafter, although unlike babysitting and pup feeding these effects are significantly different from zero later in life. Residual variation also varies across age categories, and is highest during adulthood.

Discussion

Using 19 years of individual-level behavioural observations and a multi-generational pedigree, we found significant additive genetic variance in all three major cooperative behaviours of meerkats – babysitting, provisioning, and sentinel behaviour. The presence of additive genetic variation is necessary for any response to selection (Falconer and Mackay, 1996) and, although estimates of heritability are low, our results show that these behaviours have the potential to evolve. Additive genetic effects appear to remain relatively stable over lifetimes, although the proportion of phenotypic variation in pup feeding and babysitting that is

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explained by additive genetic effects of may decline with age due to increases in residual variance.

Like previous analyses of variation in cooperative behaviour in the same population, we found strong effects of age, sex and dominance status. Contributions to cooperation increase over the first two years, peaking among yearlings and subsequently declining throughout adulthood (Clutton-Brock et al., 2002, 2000). Pup feeding contributions peak earlier in life (within the first year) relative to babysitting and sentinel behaviour, although this may be driven by variation in the quality as well as quantity of feeds. Younger individuals tend to be less competent foragers and catch smaller prey relative to older individuals (Brotherton et al., 2001; Thornton, 2008). Here we included all items in a simple count, while previous studies that used more qualitative analyses or focused only on larger, more nutritionally valuable items have shown that pup feeding of such prey peaks at later ages (>12 months; Brotherton et al., 2001; Clutton-Brock et al., 2001a). Feeding frequency in general is likely to be higher at younger ages, but actual energetic contributions to feeding pups are likely to peak later in life. More broadly, the increase in contributions to all forms of cooperative behaviour over the first two years of life may be aligned with increased foraging ability over the same period; previous studies suggest that contributions to cooperative behaviour are positively associated with individual condition (Clutton-Brock et al., 2002; Russell et al., 2003b), which itself tends to increase rapidly over the first two years before stabilising and then declining later in life (Thorley et al., 2020).

Both dominant and subordinate males contribute less to babysitting and provisioning pups relative to females, but spend more time on sentinel behaviour (Clutton-Brock et al., 2002, 2001a). These sex differences have been attributed to variation in philopatry in this species and

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may occur because females derive greater direct benefits than males from raising recruits to their natal group. Alternatively, they may be connected to the role played by males in chasing off intruders or, in the case of younger males, to their acquisition of information on neighbouring groups that they might subsequently join. Across both sexes, dominant individuals contribute less to babysitting and provisioning pups relative to subordinates (Clutton-Brock et al., 2004, 1998), consistent with the suggestion that dominants may maximise their fitness by prioritising future breeding attempts over the short-term energetic costs of cooperative behaviour (and that subordinates might thereby gain indirect fitness). The dominant males also commonly guard access to the dominant female, which probably affects their contributions to babysitting. Individual contributions are lower in larger groups for each behaviour, and we find greater contributions in both babysitting and pup feeding when litter sizes are larger (Clutton-Brock et al., 2001c, 1998). These trends likely illustrate the flexibility of cooperative behaviour, as individuals adjust their contributions based both on the demands of pups and the supply from other group members.

Consistent individual differences in behaviour (quantified as the repeatability of behaviour, and often termed 'animal personality') have been found in many taxa (e.g., Bell et al., 2009), including some cooperatively breeding species (Bergmüller et al., 2010). Since individual contributions to cooperative behaviours need to change as the demands of pups increase and then fall and are also likely to be affected by load sharing with other adults (Brotherton et al., 2001; Clutton-Brock et al., 2001a), it is unsurprising that there was only moderate repeatability of individual contributions to babysitting and provisioning. Our estimates of repeatability for these behaviours are lower than those of a previous study in this population (English et al., 2010), although this is likely driven by differences in model specification (in particular, that our

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models enable partitioning of variation due to shared group effects across several time periods that might otherwise be attributed to consistent differences among individuals across the population). Individual differences may be generated by a variety of processes, including developmental and early life effects, stable environmental or social variation, maternal effects, and additive genetic effects. While we found little evidence for maternal effects overall (either genetic or environmental), the shared early life environment (focal individual's litter) was a significant source of variance for all behaviours. This indicates that the early life environment, comprising various factors including the size and status of the group when a litter was born, exerts an influence on the future behaviour of all individuals within the litter. By contrast, we do not find any important 'permanent environment' effects, which are specific to each individual and last throughout their lifetimes. Individuals do, however, show repeatable variation within breeding seasons, leading to higher 'short-term repeatability'. Another study in this population found that individuals that show high levels of helping behaviour at one breeding event tend to reduce helping in the subsequent event (Russell et al., 2003b); our findings do not refute this but instead suggest that such within-individual variation may actually be relatively small in comparison to among-individual variation across the course of the breeding season.

There were significant additive genetic effects underlying the observed phenotypic variation in all three components of cooperative behaviour, although in all cases the heritability was low. This is consistent with some previous estimates of the heritability of contributions to cooperative behaviours. In long-tailed tits (*A. caudatus*) the heritability of provisioning effort of both parents and helpers is also low across all years (<0.1; Adams et al., 2015), while all three major forms of helping behaviours performed by the cooperatively breeding cichlid *N. pulcher* showed effectively zero heritability (Kasper et al., 2017a). In contrast, two studies that have

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explored the heritability of threshold effects (i.e., the decision of whether to help or not during a given breeding season) have shown much higher levels of heritability. In western bluebirds (*S. mexicana*), heritable differences accounted for over 75% of the phenotypic variance in whether individuals helped at a nest (noting that only a small proportion of individuals - 1.3% of females and 6.5% of males - were helpers; Charmantier et al., 2007). Variation in the delay of dispersal (a prerequisite for becoming a helper) is highly positively correlated between sires and male (although not female) offspring in a small sample of red wolves (*Canis rufus*), suggesting a strong genetic component (Sparkman et al., 2012).

Behavioural heritabilities are generally thought to be lower than morphological trait heritabilities (Mousseau and Roff, 1987) and to compare our results for meerkats with those from studies of other wild mammals we compiled estimates of the heritability of social and non-social behaviour and of life history and morphological traits from other quantitative genetic studies of natural populations of mammals (see Supporting Information File S3 for full details of the literature search and Supporting Information File S4 for the collated information). As expected, the heritability of behaviour tends to be lower than that of morphological traits (Figure 3; Tables S13-S14). Heritability estimates of social behaviour are often particularly low and frequently non-significant. The heritabilities of cooperative behaviour that we describe in meerkats are also low relative to other behavioural traits in other species. For example, estimates compiled by Stirling et al. (Stirling et al., 2002) show that mean heritabilities across seven categories of behaviour ('Anti-predator', 'Reproductive', 'Foraging', 'Temperament', 'Movement', 'Social', and 'Other') range from 0.29 to 0.33, and a more recent meta-analysis estimated the mean heritability of behaviour at 0.235 (Dochtermann et al., 2019).

The relatively low heritability of social behaviours is possibly because the expression of a focal individual's behaviour is determined – at least in part – by interactions with one or more social partners or neighbours (Moore et al., 1997). Low heritabilities can arise if a disproportionately large amount of phenotypic variation can be attributed to environmental sources (both measured and unmeasured). When behaviours are expressed in a social context, individuals may adjust their trait expression not only on the basis of their own intrinsic state but also in response to the behaviour of other individuals within the group (Bailey et al., 2018; Webster and Ward, 2011). The social environment is also likely to be more variable than the general physical environment, especially over short timescales. Such effects can be seen in the strong contribution of the shared current environment to observed phenotypic variation, particularly in pup feeding. Our results further suggest that, while additive genetic effects remain relatively stable over lifetimes, the heritability of pup feeding and babysitting in particular may decline with age due to increases in residual variance. Age-related increases in residual (or 'unexplained') variance could be due to an accumulation of small environmental effects over time, such that non-systematic variability in behaviour may vary as a result of age and prior experience (Stamps et al., 2012). The changes in residual variance are not offset by the declining effect of the shared litter environment after the first year of life. Increased social experience with age could lead to more variation in how individuals adjust their behaviour to specific situations – for example by reducing their effort when other individuals contribute more, thereby increasing within-group variance during any single period. A recent study in this population indicates that such 'inequality' among individuals can vary with both age and group size, and thus may inflate within-group variation accordingly (Rotics and Clutton-Brock, 2021). We also find that unmeasured shared social environment effects (i.e., group-level effects above and beyond the size of both the group and the litter, such as current group composition) have strong short-term effects here, particularly on pup feeding behaviour. It is perhaps unsurprising

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that these shared effects explain less variation in sentinel behaviour and babysitting relative to pup feeding given that these former behaviours are usually performed by one individual at a time, thus variation among groups is likely to be driven largely by group size (i.e., individuals in larger groups contribute less on average). Group-level differences in pup feeding are likely to be affected by a number of other unmeasured variables in addition to the effects of group size, such as territory quality and group differences in social structure – both of which are liable to lead to variation in foraging success, and thus 'generosity'. Litters may also vary in how demanding they are: pups follow adults and beg noisily for food to signal their hunger, increasing their likelihood of being fed (Brotherton et al., 2001). The behaviour of other individuals, both adults and pups, can therefore have a strong effect on the expression of a focal individual's helping behaviour.

The effects of the social environment can also play a major role in the evolution of social systems. If variation in the social environment reflects (at least in part) genetic differences among individuals, then indirect genetic effects (IGEs) may be important. That is, the effects of the social environment include a heritable component because the social environment is itself created by the traits of conspecifics (Moore et al., 1997). IGEs can contribute to the evolutionary response to selection and can alter the evolutionary dynamics of traits compared to expectations under quantitative genetic models that include only direct genetic effects (such as presented here). For example, a positive correlation between direct genetic effects (the contribution of an individual's own genes to its phenotype) and indirect genetic effects (the contribution of an individual's genes to another individual's phenotype) can greatly increase the total heritable variation available to selection (e.g., Bergsma et al., 2008; Bijma et al., 2007; Ellen et al., 2008). IGEs can have important effects on the response to selection both independently

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from and in interaction with genetic relatedness between individuals (McGlothlin et al., 2010), which is the central parameter in kin selection models that investigate the evolutionary consequences of social interactions (Queller, 1992). It is therefore likely that incorporating both relatedness and IGEs will be important when modelling social evolution in cooperatively breeding species (Bijma and Wade, 2008; McGlothlin et al., 2010). Meerkats live in highly related groups (mean coefficient of relatedness r = 0.34), meaning that – although they are considered to be 'indiscriminate altruists' – helpers are often highly related to the recipients of their cooperative contributions (Duncan et al., 2019). We found some significant effects of relatedness between focal individuals and the litters being fed or babysat, although further investigation is required to determine whether this is driven by relatedness directly or by variation among categories within a group's structure, e.g., lower contributions by immigrant males.

Despite increasing interest in how IGEs may shape behavioural phenotypes in animal societies, empirical studies remain relatively scarce (Bailey et al., 2018). This scarcity is likely a result of the complexity of the modelling framework that is needed and associated data requirements (Bijma, 2010a, 2014; McGlothlin and Brodie, 2009). Among cooperative breeders, the only study thus far to have investigated the role of IGEs in variation in cooperative behaviour (offspring provisioning rates in long-tailed tits, *A. caudatus*; Adams et al., 2015) did not find any evidence for them. Despite a relatively large sample size, well-structured pedigree and a tractable group size (an upper limit of 5 helpers per nest), the study was still likely underpowered to detect IGEs (Bijma, 2010a). The large and varying group sizes such as those observed in meerkats present additional difficulties in the estimation of IGEs (Bijma, 2010b; Hadfield and Wilson, 2007), but are important to consider as the size of the interacting group

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can affect not only the total heritable variance and response to selection but also the magnitude of IGEs themselves. The evolutionary effects of IGEs can be accelerated in larger groups because of the potential for feedback that can occur when traits in two or more individuals simultaneously affect one another (McGlothlin et al., 2010). However, it is also the case that an individual's IGE on another given individual is probably diluted in larger groups for the simple reason that interactions between a specific pair of individuals is likely to be less intense (Bijma, 2010b). The degree of dilution is likely to be specific to traits and populations, and thus the effect of group size on IGEs needs to be estimated with empirical data.

While the level of (direct) genetic variance we find is low, it need not be the case that indirect genetic effects harbour similar levels of additive genetic variance – particularly as it is not always clear exactly how social effects on a given trait are generated. For example, a focal individual's contribution to pup feeding may depend not only upon its own state and the contributions of other individuals but also the level of begging from pups and the relative size or social status of other individuals within the group. Indeed, a remaining puzzle for IGE studies is to determine the pathways through which interactions among traits belonging to different individuals are mediated (Kruuk and Wilson, 2018; McGlothlin and Brodie, 2009). Previous work in this population suggests a link between body size and/or weight gain and variation in cooperative contributions (Clutton-Brock et al., 2002; Duncan et al., 2019), thus differences in morphological traits (that can harbour greater amounts of heritable variation; Huchard et al., 2014; Nielsen, 2012) may also generate differences in behaviour among conspecifics.

In this study, we have demonstrated repeatable variation among individuals that is driven by the presence of significant additive genetic variance in three cooperative behaviours in a natural

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population of cooperatively breeding mammals. These cooperative behaviours therefore have the potential to mount an evolutionary response to selection. We also found effects of group size and of the shared group environment (which includes unmeasured social effects) on the expression of these behaviours. Together, these results also suggest a possible role for indirect genetic effects in determining the total heritable variation (and so the response to selection) in cooperative behaviour in this population. While we found no evidence for age-related changes in additive genetic variation, the increase in residual variation at later ages suggests that heritability (and thus the potential evolutionary response to selection) may decline with age. Further investigation into the drivers of this variation may be informative – for example, a recent study using this population suggests that older individuals are more sensitive to the social environment (Rotics and Clutton-Brock, 2021), which may add further complexity to empirical estimation of the role of indirect genetic effects. The application of powerful and flexible modelling techniques to studies of cooperative breeders is thus likely to prove an important next step in our understanding of the evolutionary dynamics of cooperative behaviour.

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Data sharing and data accessibility

Data and code for reproducing the main analyses are available through the Dryad Digital Repository database (https://doi.org/10.5061/dryad.cfxpnvx68). The data and code for the meta-analysis of heritability estimates of selected traits in wild mammals is available in Supporting Information (Files S3-S5).

FIGURES

Figure 1: Average contributions to three cooperative behaviours (A-C: babysitting; D-F: pup feeding; G-I: sentinel behaviour) vary with age and sex (middle column) and group size (right column). A: Babysitting – an adult meerkat remains with the dominant breeding female's pups at the burrow while the rest of the group go out to forage (photo by T. Houslay); D: pup feeding – a pup eats a scorpion given to it by the adult in the background (N. Harrison); G: sentinel behaviour – an adult meerkat stands guard from a raised position while the group forages (T. Houslay). On data panels, lines show predictions from statistical models (95% credible intervals in shaded areas). Points are raw data shown with low opacity to illustrate areas of high density. Panels B, E, H (middle column): colour indicates sex. Panels C, F (right column): colour indicates 3 representative sizes for the litter being babysat / fed. Predictions average over the effects of other continuous variables, and are shown for subordinates (all data panels) and subordinate females where sex is not shown separately (panels C, F, I).
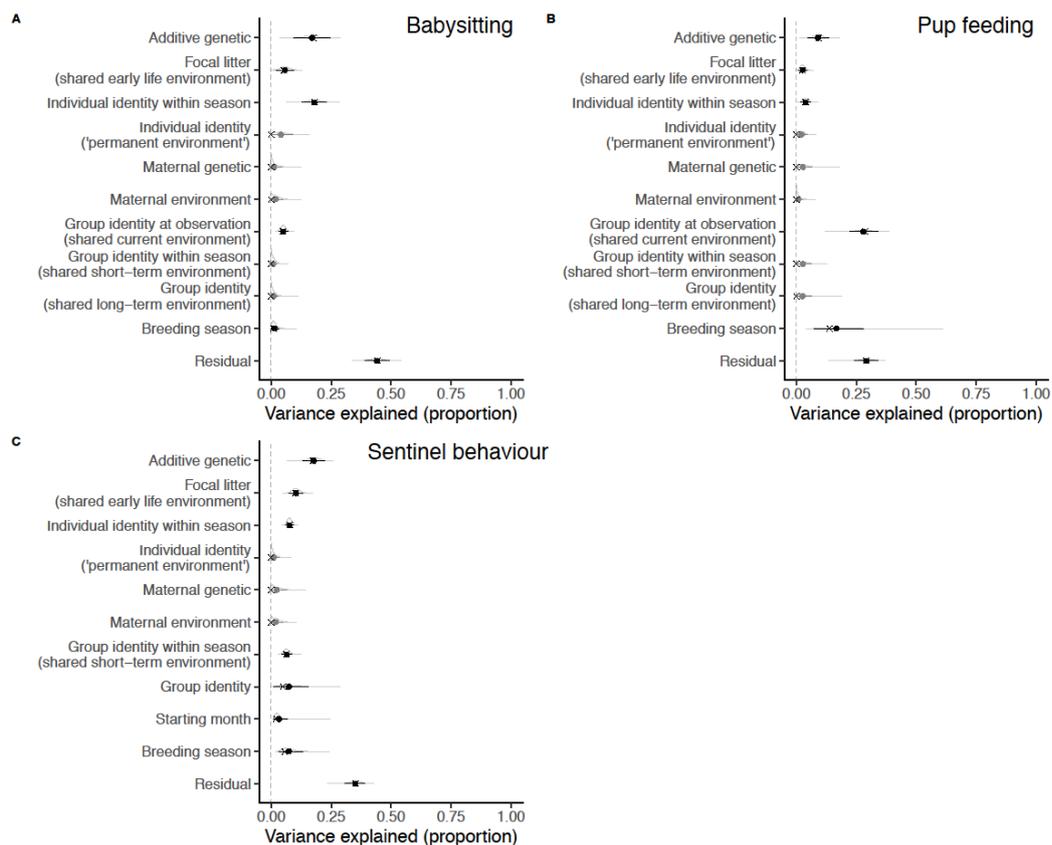
Figure 2: Contributions of genetic and non-genetic sources to phenotypic variation in cooperative behaviours (shown as proportion of phenotypic variance on the link scale, excluding fixed effects variance; A: babysitting; B: pup feeding; C: sentinel behaviour). Points and bars show posterior means with 95% credible intervals, with crosses showing the posterior modes. Black points indicate 'important' effects, where the posterior mode was above the lowest 25% quartile of the range, while grey points indicate effects that do not meet this criterion. Grey distributions show the full posterior density.
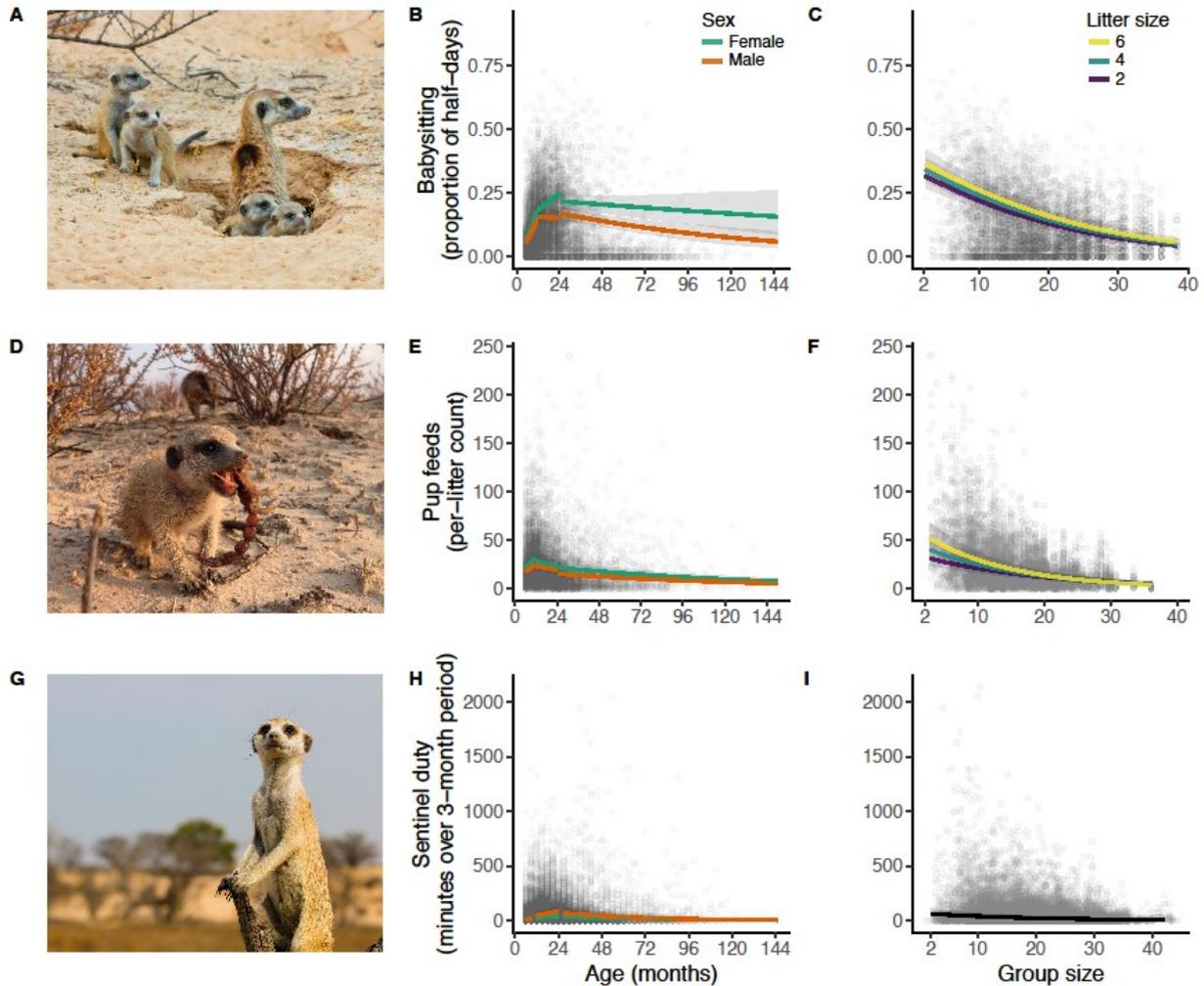
Figure 3: Published heritability estimates (points with 95% confidence intervals where available and truncated at 0,1 for visualisation purposes) for behavioural (non-social and social), life history and morphological traits in natural populations of mammals. Behaviours were classified as 'social' if described as such in the original studies. Black points indicate statistically significant values, grey points non-significant (as assessed in the original studies). Open circles denote heritability values published without estimates of uncertainty (18 data points from 4 studies) and thus excluded from our analysis, but shown here for completeness.

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Large red points and bars show the predicted value and 95% credible intervals for each category from a simple meta-analysis (see Supporting Information File S3 for details). Morphological heritabilities are significantly higher than all other categories shown here (none of which differ significantly from one another; see Tables S13-S14). The 166 estimates shown here are taken from 41 studies of 19 populations of 18 mammal species (Supporting Information File S4). Summary of data: non-social behaviour, n = 23, mean = 0.18, median = 0.09, range = 0.001-0.7; social behaviour, n = 35, mean = 0.08, median = 0.07, range = 0-0.32; life history, n = 51, mean = 0.19, median = 0.14, range = 0-0.81; morphology, n = 57, mean = 0.33, median = 0.25, range = 0.02-0.87.
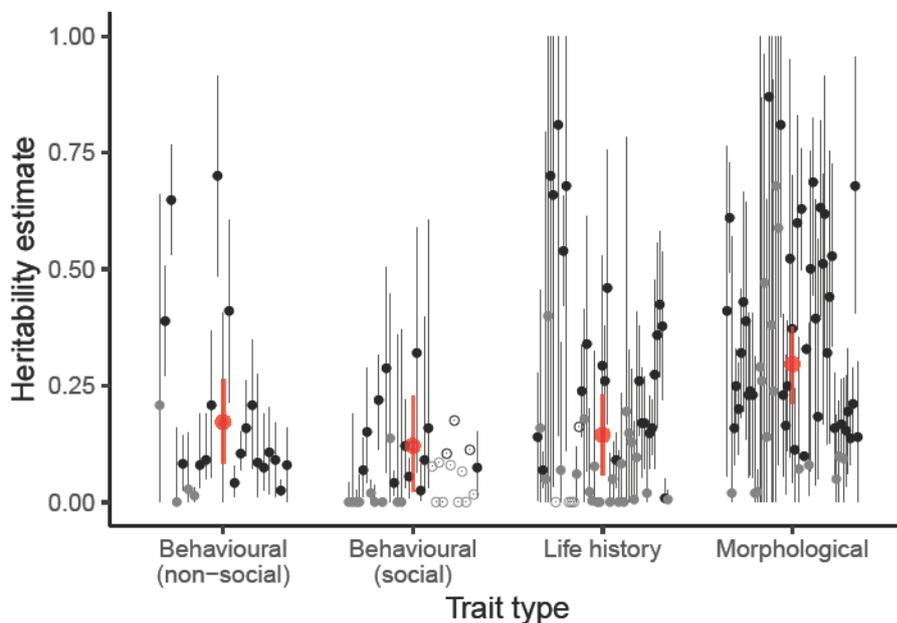
TABLES

Table 1: Additive genetic variance (V_a), phenotypic variance (V_p) and variance due to fixed effects (V_f), shown as mean values with 95% credible intervals from highest posterior density distributions, for each of the three cooperative behaviours. Heritability (h^2) is estimated on the liability scale for babysitting and the observed scale for pup feeding and sentinel behaviour, and shown both excluding and including the fixed effects variance.

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Behaviour	V_a	V_p	V_f	h^2	
				No V_f	With V_f
Babysitting	0.12 (0.06; 0.18)	0.72 (0.66; 0.78)	0.80 (0.73; 0.86)	0.07 (0.04; 0.10)	0.05 (0.03; 0.07)
Pup feeding	0.06 (0.03; 0.09)	0.67 (0.57; 0.78)	1.22 (1.10; 1.33)	0.06 (0.03; 0.09)	0.05 (0.03; 0.08)
Sentinel behaviour	0.69 (0.50; 0.86)	3.93 (3.49; 4.41)	1.61 (1.50; 1.71)	0.01 (0.01; 0.02)	0.01 (0.01; 0.02)

Table 2: Selected estimated variance-covariance matrices from models for (A) babysitting, (B) pup feeding, and (C) sentinel behaviour where some variance components were allowed to vary and covary across age classes (<12 months, sub-adult; 12-24 months, yearling; 24+ months, adult). The upper block presents additive genetic effects, the middle block the shared early life environment effects (litter identity of the focal individual), and lower block the residual variance. Within each block, variances are shown on the shaded diagonal, covariances below the diagonal, and correlations above. Estimates give the mean and 95% credible intervals from the posterior distribution.

	(A) Babysitting			(B) Pup feeding			(C) Sentinel
	Sub-adult	Yearling	Adult	Sub-adult	Yearling	Adult	Sub-adult

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Additive genetic	Sub-adult	0.17 (0.08,0.27)	0.91 (0.77,1.00)	0.90 (0.75,1.00)	0.11 (0.07,0.15)	0.96 (0.90,1.00)	0.95 (0.86,1.00)	0.87 (0.67,1
	Yearling	0.12 (0.05,0.19)	0.11 (0.03,0.18)	0.91 (0.76,1.00)	0.09 (0.05,0.12)	0.08 (0.04,0.12)	0.97 (0.90,1.00)	0.83 (0.68,0
	Adult	0.17 (0.08,0.26)	0.13 (0.06,0.22)	0.21 (0.08,0.34)	0.11 (0.06,0.15)	0.10 (0.05,0.14)	0.12 (0.05,0.19)	0.75 (0.58,0
Focal litter	Sub-adult	0.16 (0.10,0.22)	0.13 (-0.58,0.83)	0.10 (-0.62,0.75)	0.06 (0.03,0.08)	0.15 (-0.29,0.57)	0.05 (-0.70,0.78)	1.22 (0.96,1
	Yearling	0.006 (-0.01,0.03)	0.01 (0.00,0.03)	0.29 (-0.57,0.96)	0.005 (-0.01,0.02)	0.02 (0.00,0.03)	0.14 (-0.64,0.85)	0.26 (0.13,0
	Adult	0.007 (-0.03,0.05)	0.007 (-0.01,0.03)	0.03 (0.00,0.09)	0.002 (-0.01,0.02)	0.002 (-0.01,0.01)	0.01 (0.00,0.03)	0.10 (-0.05,
Residual	Sub-adult	0.16 (0.12,0.20)			0.07 (0.06,0.09)			1.28 (1.17,1
	Yearling		0.25 (0.21,0.29)			0.13 (0.12,0.15)		
	Adult			0.66 (0.56,0.76)			0.44 (0.39,0.48)	

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