



The origins of consistent individual differences in cooperation in wild banded mongooses, *Mungos mungo*



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Individual differences in contributions to cooperation can be strikingly consistent over time giving rise to alternative cooperative phenotypes within animal societies. Following the social niche specialization hypothesis, these consistent differences may be driven by social conflict over reproductive opportunities if individuals specializing as 'breeders' and 'nonbreeders' experience a beneficial reduction in social conflict and differential costs associated with cooperating. This hypothesis gives three testable predictions: (1) consistent individual differences in cooperative behaviour will be accompanied by consistent individual differences in reproductive behaviour, (2) individuals contributing heavily to reproduction will contribute relatively little to cooperative behaviours within the same breeding attempt and vice versa, and (3) individuals that consistently contribute heavily to reproduction over their lifetime will also consistently contribute less to cooperative behaviours and vice versa. We tested these predictions with a 15-year investigation into the lifetime patterns of mate guarding and two forms of cooperative offspring care ('babysitting' and 'escorting') in a wild population of banded mongooses. We found significant repeatability of individual contributions to both cooperative behaviours, as well as significant repeatability of individual levels of mate guarding. However, we found no evidence of negative covariance between contributions to cooperative and reproductive behaviours either within breeding attempts or across lifetimes. This suggests that the observed consistent individual differences in both cooperative behaviour and reproduction are not associated; there is no evidence of a trade-off between reproduction and cooperation. However, we found a significant positive covariance between babysitting and escorting when estimated both within breeding attempts and across lifetimes, which suggests that some group members are generally more cooperative than others, contributing more to both behaviours over their lifetimes. The drivers of this consistent individual variation in contributions to cooperation remain unknown.

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Within animal societies there is striking variation in how much individuals invest in cooperative activities (Komdeur, 2006). Individual variation in contributions to cooperation may be attributable to differences in individual characteristics such as energetic state (e.g. Arabian babblers, *Turdoides squamiceps*: Wright, Maklakov, & Khazin, 2001), inheritance rank (e.g. paper wasps, *Polistes dominulus*: Cant & Field, 2001), sex (e.g. meerkats, *Suricata suricata*: Clutton-Brock et al., 2002) and age (e.g. banded mongoose: Hodge, 2007). However, individual differences in

contributions to cooperation can also be consistent over time and persist after these differences have been accounted for (e.g. meerkats: Carter, English, & Clutton-Brock, 2014; English, Nakagawa, & Clutton-Brock, 2010; cichlids, *Neolamprologus pulcher*: Bergmüller & Taborsky, 2007; Le Vin, Mable, Taborsky, Heg, & Arnold, 2011; western bluebirds, *Sialia mexicana*: Charmantier Keyser, & Promislow, 2007; see review in Bergmüller, Schürch, & Hamilton, 2010). Although the causes of consistent individual differences in behaviour have received growing attention in recent years (Bergmüller et al., 2010; Dall, Bell, Bolnick, Ratnieks, & Sih, 2012; McNamara, Stephens, Dall, & Houston, 2009; Wright, 2007), it still remains unclear why individuals should exhibit such consistent behavioural differences within the context of cooperation (Carter et al., 2014).

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The social niche specialization hypothesis (Bergmüller & Taborsky, 2010) suggests that consistent individual differences in behaviour will be favoured where (1) there is within-group conflict over limited resources such as food, space or breeding opportunities, (2) there are fitness benefits to niche specialization as it reduces this conflict, and (3) there are costs to switching between behaviours which create positive feedback on behavioural expression (e.g. if changing behaviour leads to escalated conflict or requires changes in physiology). Within cooperatively breeding species, high reproductive skew means that there is great potential for within-group conflict over reproductive opportunities. Following the social niche specialization hypothesis, this conflict over reproductive opportunities may be reduced by the differentiation of individuals into alternative, potentially lifelong, social niches (e.g. as 'breeders' and 'nonbreeders'). Indeed, stable social hierarchies and consistent monopolization of breeding opportunities by one (or a few) dominant individual(s) means that escalated conflict is rarely observed. While the social niche specialization hypothesis may explain why individuals settle into specialized roles within the context of reproduction, whether it can also explain consistent individual differences in the contributions to cooperation remains unknown.

Individual contributions to different behaviours may be correlated where specialization within the context of one behaviour affects the costs and benefits associated with another (Bergmüller & Taborsky, 2010). Specialization in lifelong roles as 'breeders' and 'nonbreeders' may determine individual contributions to cooperative offspring care where individual differences in the likelihood of gaining reproductive success generate differences in the fitness costs associated with cooperating. For example, breeding individuals will experience higher fitness costs than nonbreeding individuals when contributing to cooperative offspring care because of missed mating opportunities (Hodge, 2007; Young, Carlson, & Clutton-Brock, 2005). Indeed, this is not a novel idea, as it has long been hypothesized that there may be 'aid behavioural syndromes' within cooperative societies whereby some individuals follow trajectories that favour indirect fitness benefits rather than trying (and failing) to reproduce themselves (West-Eberhard, 1975, p. 16). Thus, role specialization with regard to reproduction has the potential to generate consistent individual differences in contributions to cooperation. Such role specializations would also generate cooperatively breeding societies that consist of individuals with lifelong specializations to positions on a continuum between 'breeders' and 'helpers', akin at its extreme to the morphological castes seen in some eusocial insects (Wilson, 1979).

The hypothesis that consistent individual differences in cooperation (and reproduction) are attributable to social niche specialization makes three predictions (Bergmüller & Taborsky, 2010). First, there will be consistent individual differences in contributions to both cooperative and reproductive behaviours across the life span (i.e. behaviours will be repeatable). Second, when an individual contributes heavily to reproduction within a breeding attempt they will contribute relatively little to cooperative offspring care and vice versa (i.e. negative within-individual covariance between contributions to cooperative and reproductive behaviours). Third, if there are consistent individual differences in contributions to both cooperative and reproductive behaviours, individuals contributing more to reproduction over their lifetime will contribute less to cooperative offspring care (i.e. negative between-individual covariance between contributions to cooperative and reproductive behaviours). Here, we tested all three predictions with a 15-year investigation into the lifetime patterns of cooperation and reproduction of a wild population of banded mongooses.

Banded mongooses differ from most cooperatively breeding species as they do not have a clear dominant breeding pair. Rather, each group generally contains a 'core' of breeding adults (one to five females and three to seven males) and a subset of younger individuals that breed occasionally (Cant, Hodge, Bell, Gilchrist, & Nichols, 2010; Nichols, Amos, et al., 2012; Nichols, Bell, Hodge, & Cant, 2012; Nichols, Jordan, Jamie, Cant, & Hoffman, 2012). Although contributions to cooperative offspring care are skewed towards younger individuals (Cant, 2003; Hodge, 2007), all individuals, including current breeders, assist in rearing communal litters (Gilchrist & Russell, 2007). Previous studies on the consistency of cooperation in other species have been limited to nonbreeding individuals and how individual cooperative tendencies predict the likelihood of dispersal (Schurch & Heg, 2010) or gaining a dominant breeding position (Carter et al., 2014). In contrast, the banded mongoose study system allows us to investigate the consistency of, and covariances between, cooperative and reproductive behavioural traits across individual lifetimes as male banded mongooses are involved in both reproduction and cooperative offspring care at all ages (Fig. 1). This provides the opportunity to test all three predictions outlined above and thereby provide novel insight into the evolution of consistent individual differences in cooperative societies.

METHODS

Study Species

Banded mongooses are small (<2 kg) diurnal herpestids that live in stable cooperatively breeding groups of 10–30 individuals (Cant, Vitikainen, & Nichols, 2013). Up to 12 adult females give birth synchronously (Hodge, Bell, & Cant, 2011) to large litters (1–20 pups; Gilchrist, 2006) up to five times a year. Our current study focused on male banded mongooses as they exhibit conspicuous behaviours associated with both reproduction and cooperative offspring care (Cant, 2003; Hodge, 2007; Nichols, Amos, Cant, Bell, & Hodge, 2010). During each synchronized oestrus period, dominant males guard particular females ('mate guarding') and aggressively chase off rival males to increase their chances of gaining parentage (Nichols et al., 2010). There are two highly conspicuous forms of pup care: (1) 'babysitting', when one or more individuals remain at the den to care for the pre-emergent pups (ages 0–4 weeks) while the remainder of the group are foraging (Cant, 2003), and (2) 'escorting', whereby each postemergence pup (aged 5–10 weeks) forms a stable dyadic relationship with a single adult 'escort' who then feeds, plays with, protects, grooms and generally cares for the associated pup until it reaches independence (Gilchrist, 2004). Although contributions to babysitting, escorting and mate guarding vary with age, individuals of all ages can and do contribute to all three behaviours (Fig. 1a). The high frequency of breeding attempts within banded mongoose societies means that group oestrus often overlaps directly with the pup care period (Fig. 1b). This is understood to underlie a direct trade-off between mating effort and cooperative offspring care as males cannot care for pups at the same time as guarding oestrous females (Hodge, 2007).

Study Site and Data Collection

This study was conducted between April 2003 and April 2014, on the Mwera Peninsula in Queen Elizabeth National Park, Uganda (0°12'S, 27°54'E). Details of vegetation and climate are given elsewhere (Cant et al., 2013). All individuals were habituated to the presence of observers at a distance of 2–4 m, enabling the collection of detailed behavioural observations without any measurable

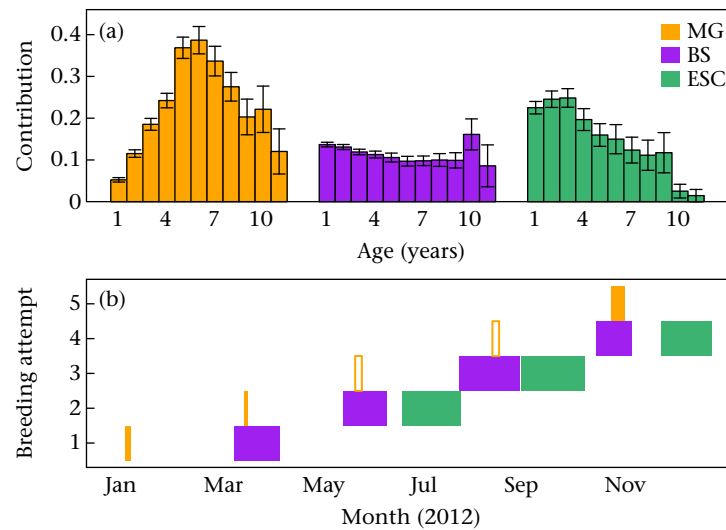


Figure 1. Patterns of individual contributions to mate guarding (MG), babysitting (BS) and escorting (ESC) (a) with increasing age (in years) and (b) across a year. (a) Bars show mean contribution (measured as the proportion of days per breeding attempt on which that behaviour was observed by any individual in the group) per age in years and lines show SEs. Contributions to mate guarding peak at 6 years of age whereas contributions to both babysitting and escorting peak at an earlier age (1 and 3 years, respectively). Larger SEs occur in older age categories because of smaller sample sizes caused by mortality and dispersal. (b) Filled blocks show periods during which behavioural traits were observed in pack '1B' during 2012; empty blocks show periods of inferred oestrus 60 days prior to birth (where no mate guarding was observed). Note that breeding attempt 1 has no escorting period because of complete litter failure during the babysitting period. Multiple overlapping breeding attempts occur within a year with overlapping periods of oestrus and offspring care.

effect of observer presence (Cant et al., 2013). Research was carried out under permit from the Uganda Wildlife Authority and the Uganda National Institute for Science and Technology.

All individuals in the population were marked with either colour-coded collars (7 g) or unique shave patterns to enable identification in the field. Collars and shaves were maintained by trapping individuals every 3–6 months, although individuals in highly habituated groups could have their hair trimmed without capture. One or two individuals within each group were fitted with a radiocollar weighing 27 g (Sirtrack Ltd., Havelock North, New Zealand) with a 20 cm whip antenna (Biotrack Ltd., Dorset, U.K.). Individuals were trapped using box traps (67 × 23 cm and 23 cm high; Tomahawk Live Trap Co., Tomahawk, WI, U.S.A.), and anaesthetized using either isoflurane or ketamine (details of trapping protocol are given elsewhere; isoflurane: Jordan, Mwanguhya, Kyabulima, & Cant, 2010; ketamine: Hodge, 2007). In total, 6794 individual capture events were carried out during the course of this study. Mongooses suffered no ill effects as a result of capture and remained fully habituated to observers following this procedure.

Behavioural Observations

Mate guarding

A total of 2916 measures of mate guarding were available from 305 male banded mongooses over 269 group oestrus periods in 11 social groups. The group oestrus period (i.e. the time from the first to the last day on which mate guarding was observed in a particular breeding attempt) lasted 5.07 ± 0.54 days (mean \pm SE). During group oestrus each female is closely followed and guarded by a single male 'mate guard' for periods that last from several hours to several consecutive days. Mate-guarding behaviour is conspicuous and easy to identify subjectively, rather than by using objective measures such as nearest-neighbour distance (Cant, 2000; Nichols et al., 2010). Groups were visited daily during group oestrus periods and all males in the group were classified for that observation session as mate guards or nonmating males (Cant, 2000; Nichols et al., 2010). The number of observation sessions per oestrus period was 3.78 ± 0.16 (mean \pm SE; range 1–14) and an individual

contribution to mate guarding per oestrus period was defined as the proportion of observation sessions that an individual was observed mate guarding.

Babysitting

In total, 2931 measures of babysitting were available from 361 male banded mongooses over 317 breeding attempts in 14 social groups. The babysitting period (i.e. the time from when pups were born to when pups emerged to forage with the group) lasted 32.33 ± 3.50 days (mean \pm SE). This babysitting period is characterized by the presence of 'babysitters': adults that remain at the den each time the group leaves on a foraging trip to protect the pups from predation or intergroup infanticide (Cant, 2003). Groups were visited every 1–2 days (once or twice per day) during each babysitting period and identities of babysitters were noted. During each observation session the foraging group was first located using telemetry and then the identity of individuals present was recorded. Banded mongooses do not exhibit roaming behaviours and always stay together as a group unless they are babysitting offspring at the den. Therefore, any individuals not present in the group could be assumed to be babysitters (Hodge, 2007). The radiocollared individual was occasionally found at the den and babysitters could be identified as individuals seen at the den. Observation sessions were either morning (0700–1130 hours) or afternoon (1630–1900 hours) sessions. The number of observation sessions per breeding attempt was 14.74 ± 0.58 (mean \pm SE; range 1–63) and an individual contribution to babysitting per breeding attempt was defined as the proportion of observation sessions that an individual was observed babysitting.

Escorting

In total, 1574 measures of escorting were available from 281 male banded mongooses over 157 breeding attempts in 10 social groups. Fewer observations are available for escorting than the other behavioural traits because (1) litters often die during the babysitting period and (2) observations of escorting are limited to highly habituated groups. Groups were visited every 1–2 days (once or twice per day) between pup emergence and pup

independence when associations between pups and adults were noted. Adults were scored as escorts if they were seen within 30 cm of the same pup for more than 50% of the observation period (Gilchrist, 2004). We defined an 'escorting period' as the period between the first and last observation of escorting. An individual contribution to escorting was defined as the proportion of days that an individual was recorded as an escort out of the total number of days escorting by any individual was recorded within the group. The number of observation sessions per escorting period was 13.29 ± 0.70 (mean \pm SE; range 1–39) and the escorting period lasted 27.06 ± 1.32 days (mean \pm SE).

Statistical Analyses

Multivariate models have been highlighted as a useful tool for investigating individual variation in behavioural traits as they allow direct estimation of both between- and within-individual variances and covariances (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010). Estimation of both between- and within-individual variances allows us to calculate a measure of repeatability that quantifies the consistency of individual differences in behaviour (Nakagawa & Schielzeth, 2010). Furthermore, estimation of between- and within-individual covariances allows us to simultaneously test for evidence of a trade-off between cooperation and reproduction both within and across breeding attempts (i.e. within- and between-individual covariance, respectively) while controlling for other factors known to affect behavioural traits.

We used the MCMCglmm package (Hadfield, 2010) in R version 3.1.1 (R Core Team, 2013) to fit multiple multivariate generalized linear mixed models (GLZMMs) and investigate both within- and between-individual variances and covariances for contributions to mate guarding, babysitting and escorting in male banded mongooses. In all models, these traits were fitted simultaneously as binomial responses with the number of observation sessions that an individual was noted as a mate guard, babysitter or escort as the numerator and the total number of observation sessions for each behaviour in each breeding attempt as the denominator. In all models, group size (the number of individuals aged >1 year), the number of females (aged >1 year) and an individual's age in years (both linear and quadratic terms) were all fitted as fixed effects including all interactions with 'trait'. Social group, breeding attempts and individual identities were included as random effects including all interactions with trait to control for repeated measures. We set social group and breeding attempt level random effects with an unstructured ('us') G-structure, i.e. allowing a fully factorial variance/covariance between behavioural traits between social groups and breeding attempts. The G-structure for the individual level random effect was set in each model as either unstructured or with covariances constrained to zero ('idh' structure; see below and Supplementary material 1). We used inverse-Wishart priors throughout and ran all models for 4 000 000 iterations, with a burn-in of 5000 and thinning interval of 1000. Successive samples from the posterior distribution had low autocorrelation ($r < 0.01$). The R script used for all analyses can be found in Supplementary material 2. All analyses were replicated using a univariate model approach with the lme4 package (Bates, Maechler, & Bolker, 2013), testing correlations between residuals and individual level best-linear unbiased predictor (BLUP) values which produced qualitatively similar results (see Supplementary material 3).

Are there consistent individual differences across the life span?

We calculated adjusted repeatabilities for each of our three behavioural traits on the latent scale with additive overdispersion

(R_{logitA}) following Nakagawa and Schielzeth (2010). Such adjusted repeatabilities estimate individual differences while controlling for confounding effects by including them in the model when calculating between- and within-individual variances. This repeatability is calculated as:

$$R_{\text{logitA}} = \sigma_x^2 / (\sigma_x^2 + \sigma_e^2 + \pi^2/3)$$

where σ_x^2 is the between-individual variance, σ_e^2 is the within-individual (residual) variance and $\pi^2/3$ is the distribution-specific variance of a binomial model with logit link (Nakagawa & Schielzeth, 2010). Variances assigned to other random effects (social group and breeding attempt) were not included in repeatability calculations. This allowed us to determine whether there are consistent individual differences while controlling for variance attributable to other factors such as differences between social groups and breeding attempts. We estimated the point estimate and credible intervals for each repeatability estimate as the posterior modes and highest posterior density (HPD) intervals estimated from a MCMCglmm (M1) for σ_x^2 and σ_e^2 . As we wanted to estimate repeatabilities of each behavioural trait independently we set all the between- and within-individual covariances to zero; i.e. with an 'idh' G-matrix for the individual level random effect and an 'idh' R-matrix for the residuals (note that we obtained qualitatively similar estimates of repeatability when calculating conditional repeatabilities from models including covariance between behavioural traits; see Supplementary material 1). As variance estimates are constrained between zero and one, the HPD interval is constrained to be positive. This means that it is not possible to quantitatively test the significance of repeatabilities calculated using this method. However, we can qualitatively assess whether traits are repeatable by examining whether the posterior distributions are truncated at zero. If posterior distributions show symmetrical distributions then we can assume that the true variance is nonzero and behavioural traits are considered to be repeatable.

Is there a negative within-individual covariance?

If individual specializations are negatively correlated across the contexts of reproduction and cooperative offspring care we expect to see a negative within-individual covariance between cooperative and reproductive behavioural traits: i.e. when individuals increase their contribution to babysitting and/or escorting they simultaneously decrease the amount of time spent mate guarding. The within-individual covariance is estimated by fitting an unstructured R-matrix for the residuals in the multivariate model. Note that we also fitted an unstructured G-matrix for the individual level random effect in this model to simultaneously test for covariances between individuals (see next section). We calculated both point estimates and credible intervals for the covariates between all three possible behavioural trait dyads using the posterior modes and HPD intervals of the covariances estimated in an MCMCglmm (M2). If there is a significant covariance between any of the behavioural trait dyads then the HPD interval would not overlap zero. Note that qualitatively similar results were obtained when considering individual contributions to cooperative and reproductive traits in consecutive breeding attempts where the period of offspring care in the first breeding attempt overlapped in time with the oestrus period of the second breeding attempt (see Supplementary material 4).

Is there a negative between-individual covariance?

If consistent individual differences in cooperation are attributable to social niche specialization and a reduction in conflict over reproductive opportunities we expect to see a negative between-

individual covariance between contributions to cooperative and reproductive behaviours: i.e. individuals that consistently contribute more in babysitting and/or escorting than the population mean over their lifetimes also consistently contribute less in mate guarding than the population mean. We can estimate the between-individual covariance by fitting an unstructured ('us') G-matrix for the individual level random effect. We calculated point estimates and credible intervals for the covariances between all three behavioural trait dyads as the posterior mode and HPD intervals from an MCMCglmm (M2). Covariances can be considered to be significant if the HPD intervals do not overlap zero.

RESULTS

Full models, sample sizes, estimates of the fixed effect parameters and graphical posterior distributions are all reported in [Supplementary material 1](#).

Are there Consistent Individual Differences Across the Life Span?

All three measured behavioural traits were found to be repeatable over the lifetime of male banded mongooses. Mate guarding and babysitting both showed similar repeatability estimates (mate guarding: $R_{\text{logitA}} = 0.10$, HPD interval = 0.07, 0.14; babysitting: $R_{\text{logitA}} = 0.12$, HPD interval = 0.09, 0.15; [Fig. 2](#)). Escorting was significantly more repeatable than babysitting or mate guarding over the lifetime of banded mongooses ($R_{\text{logitA}} = 0.25$, HPD interval = 0.17, 0.30; [Fig. 2](#)).

Is there a Negative Within-individual Covariance?

When mate guarding (MG), babysitting (BS) and escorting (ESC) were considered within the same breeding attempt we found no significant within-individual covariance between cooperative and reproductive behavioural traits ($R\text{-COV}_{\text{MG-BS}} = -0.03$, HPD interval = $-0.15, 0.11$; $R\text{-COV}_{\text{MG-ESC}} = -0.06$, HPD interval = $-0.67, 0.41$; [Fig. 3a](#)). However, we found a strong significant within-individual

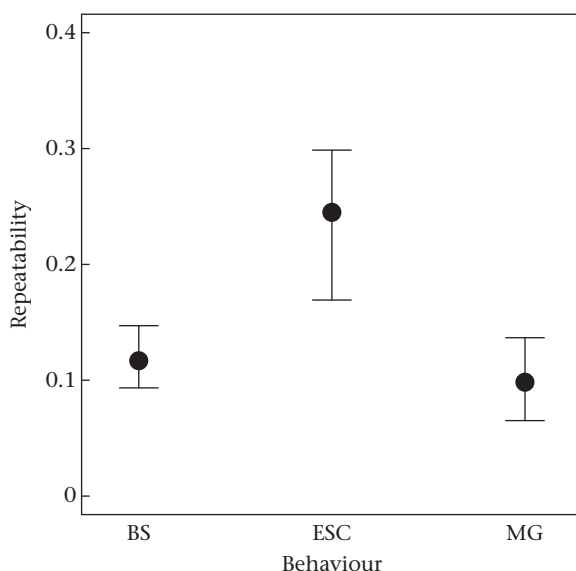


Figure 2. Adjusted repeatability estimates and credible intervals for individual contributions to two cooperative behavioural traits, babysitting (BS) and escorting (ESC), and one reproductive behavioural trait, mate guarding (MG). Estimates and credible intervals were generated from an MCMCglmm controlling for variation in age, group size and the number of females within the group.

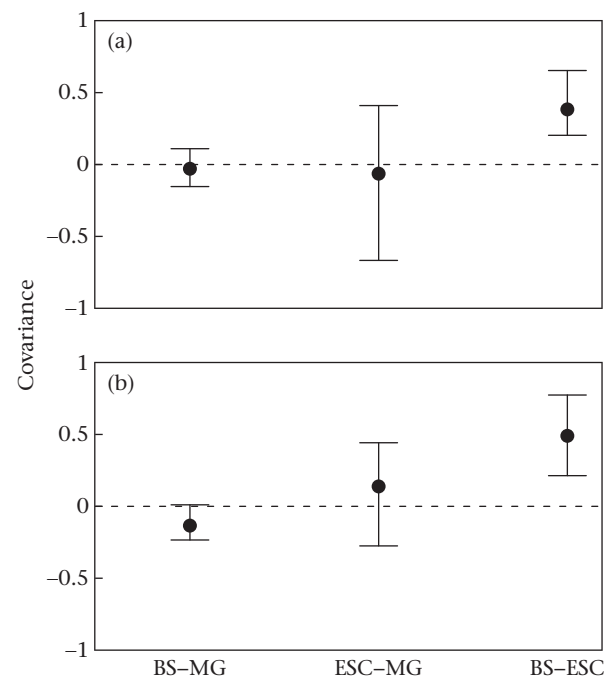


Figure 3. Covariance estimates between contributions to babysitting (BS), escorting (ESC) and mate guarding (MG) estimated (a) within individuals and (b) between individuals. Covariance estimates and confidence intervals were extracted from two separate MCMCglmm as the posterior modes and highest posterior density functions of posterior densities. Where confidence intervals do not overlap zero (dashed line) they are considered to be significant.

covariance between the two cooperative behavioural traits ($R\text{-COV}_{\text{BS-ESC}} = 0.38$, HPD interval = 0.20, 0.65; [Fig. 3a](#)) which suggests that when individuals increase their contribution to one cooperative behaviour they also tend to increase their contribution to the other.

Is there a Negative Between-individual Covariance?

Credible interval estimates for between-individual covariances between mate guarding and both babysitting and escorting overlapped zero ($\text{IND-COV}_{\text{MG-BS}} = -0.13$, HPD interval = $-0.23, 0.01$; $\text{IND-COV}_{\text{MG-ESC}} = 0.14$, HPD interval = $-0.28, 0.44$; [Fig. 3b](#)) giving no evidence that individual contributions to reproduction and cooperation are negatively correlated across breeding attempts. However, we found a strong positive between-individual covariance between babysitting and escorting ($\text{IND-COV}_{\text{BS-ESC}} = 0.49$, HPD interval = 0.21, 0.77; [Fig. 3b](#)). Thus we found no evidence that individuals specialize across their lifetime in reproduction versus helping, but we did find evidence that individuals that consistently contribute highly to babysitting also consistently contribute highly to escorting behaviours.

DISCUSSION

The social niche specialization hypothesis predicts consistent individual differences in behaviour when the differential expression of behaviour by individuals reduces social conflict and there is positive feedback on the consistent expression of behaviour ([Bergmüller & Taborsky, 2010](#)). Within cooperatively breeding societies, social conflict often arises over breeding opportunities and leads to specialization of group members into distinct social niches of breeders and nonbreeders. Here we found mate guarding, a conspicuous form of mating effort, to be repeatable over the

lifetime of male banded mongooses. Although there are no distinct lifetime roles as breeders and nonbreeders (i.e. individual differences are continuous rather than fitting into distinct categories), this repeatability means that individuals are consistent in their relative contribution to reproduction over their entire lives. Furthermore, babysitting and escorting (two forms of cooperative offspring care) were also repeatable across the lifetimes of male banded mongooses, suggesting that some individuals are specialized across their lifetimes as being more or less cooperative. The social niche specialization hypothesis would predict that individual differences in cooperative offspring care should covary negatively with individual differences in contributions to mate guarding. However, we found no evidence for a negative covariance between mate guarding and either form of cooperative offspring care when measured either within breeding attempts or across lifetimes. Our results suggest that there is no trade-off between contributions to reproduction and cooperative offspring care in male banded mongooses (but see Hodge, 2007 for females). Hence, our results do not support the hypothesis that consistency in cooperative behaviour is the result of individual specialization in reproductive roles. To explain the observed consistent differences in cooperative behaviour in this system we may need to consider other factors, such as consistent individual differences in aspects of physiology and/or the energetic costs of helping.

Previous studies of banded mongooses suggest that they are able to adjust their contributions to cooperation depending on their current energetic state and/or circulating hormone concentrations in a manner that may reduce the costs associated with caring for offspring (Hodge, 2007; Sanderson et al., 2014). However, we have shown here that despite this short-term compensation, individuals are repeatable in their contributions to both babysitting and escorting (and mate guarding) across their lifetimes. Note that in this context lifetime repeatability does not necessarily mean that individuals cooperate (or mate guard) at a consistent level throughout their lives; rather, it implies that individuals behave consistently different from the population mean across different contexts (e.g. at different ages and in different group sizes; Fig. 4). Our estimates of repeatability for babysitting (0.10), escorting (0.25) and mate guarding (0.12) are lower than the average repeatability (0.37) reported across behaviours in a wide range of taxa (Bell, Hankison, & Laskowski, 2009). Although we are unaware of any previous studies investigating consistency of mating effort over the lifetime of individuals in the wild, our estimates of repeatability of cooperative offspring care are similar to the adjusted repeatabilities reported for cooperative vigilance (0.10; Carter et al., 2014) and babysitting (0.22; English et al., 2010) in a wild population of the closely related meerkat.

We found a significant positive covariance between the two observed cooperative behavioural traits both when estimated within breeding attempts (i.e. within-individual covariance) and when estimated over lifetimes (i.e. between-individual covariance). Respectively, these findings indicate that (1) when individuals increase their contribution to babysitting they also increase their contribution to escorting, and (2) individuals that consistently contribute heavily in babysitting over their lifetimes also consistently contribute heavily in escorting (and vice versa); which may be termed a 'helping syndrome' (English et al., 2010). Such evidence of a helping syndrome is especially interesting given that the two forms of cooperative offspring care are very different. Escorting involves direct care of pups outside the den (entailing feeding, grooming and carrying; Gilchrist & Russell, 2007), while babysitting involves active defence of pups in the den from aggressive attacks by predators and neighbouring mongoose groups (Cant, 2003). This positive correlation in contributions to cooperation across different contexts is similar to that found in meerkats (Carter

et al., 2014; English et al., 2010) but contrasts with other species in which individuals have been found to specialize in cooperative roles in either vigilance or territory defence (e.g. noisy miners, *Manorina melanocephala*; Arnold, Owens, & Goldizen, 2005; eusocial insects: Wilson, 1979).

It has long been suggested that individual variation in cooperative investment within cooperatively breeding societies may be driven by a trade-off with reproductive investment (Hodge, 2007; West-Eberhard, 1975; Young et al., 2005). In this study, although we found both cooperative and reproductive behavioural traits to be repeatable across the lifetimes of male banded mongooses, we found no evidence for negative covariance between contributions to cooperation and individual differences in mate guarding. This is a surprising result given that periods of oestrus commonly overlap with periods of cooperative offspring care in this species (Fig. 1b). Indeed, this overlap between babysitting and oestrus and the predicted trade-off between babysitting and mate guarding has previously been used to explain the decreased babysitting effort observed in older males (Fig. 1a; Cant, 2003; Hodge, 2007). A more recent study suggests that older males may only babysit less than younger males during the few days of synchronized oestrus (Sanderson et al., n.d.). Therefore, any variation in individual contributions to babysitting attributable to a trade-off with mate guarding during oestrus may be overshadowed by individual variation in contributions to babysitting outside oestrus which is attributable to other factors. Thus, a more detailed study of individual contributions to mate guarding and babysitting specifically in the subset of babysitting days during oestrus periods would be expected to demonstrate negative covariance between the two traits simply because a male cannot mate guard if he is babysitting. However, even if there was a negative within-individual covariance between babysitting and mate guarding when measured only during oestrus periods, the reasons behind individual consistency in contributions into cooperative behaviour over the lifetime would still remain unknown.

If consistency of cooperation is not attributable to variation in reproductive behaviours then what is causing some individuals to be so-called 'super-helpers' (Hodge, 2007)? As an alternative to the social niche specialization hypothesis, Biro and Stamps (2008) suggested that consistent individual differences in behavioural traits may be favoured when those traits facilitate the acquisition of food resources at different rates and contribute to consistent individual differences in productivity. Although their paper focused on personality traits such as boldness and activity, the same may be true of cooperative behavioural traits if cooperation leads to a differential intake of food resources. Both babysitting and escorting are energetically expensive (Hodge, 2007; Sanderson et al., 2014) so it seems plausible that variation in cooperative effort may be associated with variation in foraging or metabolic rates. The covariance between babysitting and escorting reported here remains significant even when body mass is included in the model (see Supplementary Table S5.3) suggesting that the observed cooperative syndrome is not likely to be solely attributable to individual variation in energetic state. However, there are many other unmeasured individual attributes that may affect individual contributions to cooperative and reproductive behaviours such as heritable variation (Charmantier et al., 2007), hormone concentrations (Madden & Clutton-Brock, 2011; Sanderson et al., 2014) and/or oxidative damage (Cram, 2013; Heiss & Schoech, 2012). Consistent individual differences in contributions to cooperative and reproductive behaviours may underlie alternative life history strategies with similar fitness values; a future study investigating survival, lifetime reproductive success and estimates of inclusive fitness may test such a hypothesis. Moreover, consistent individual differences in different behaviours may be driven by different

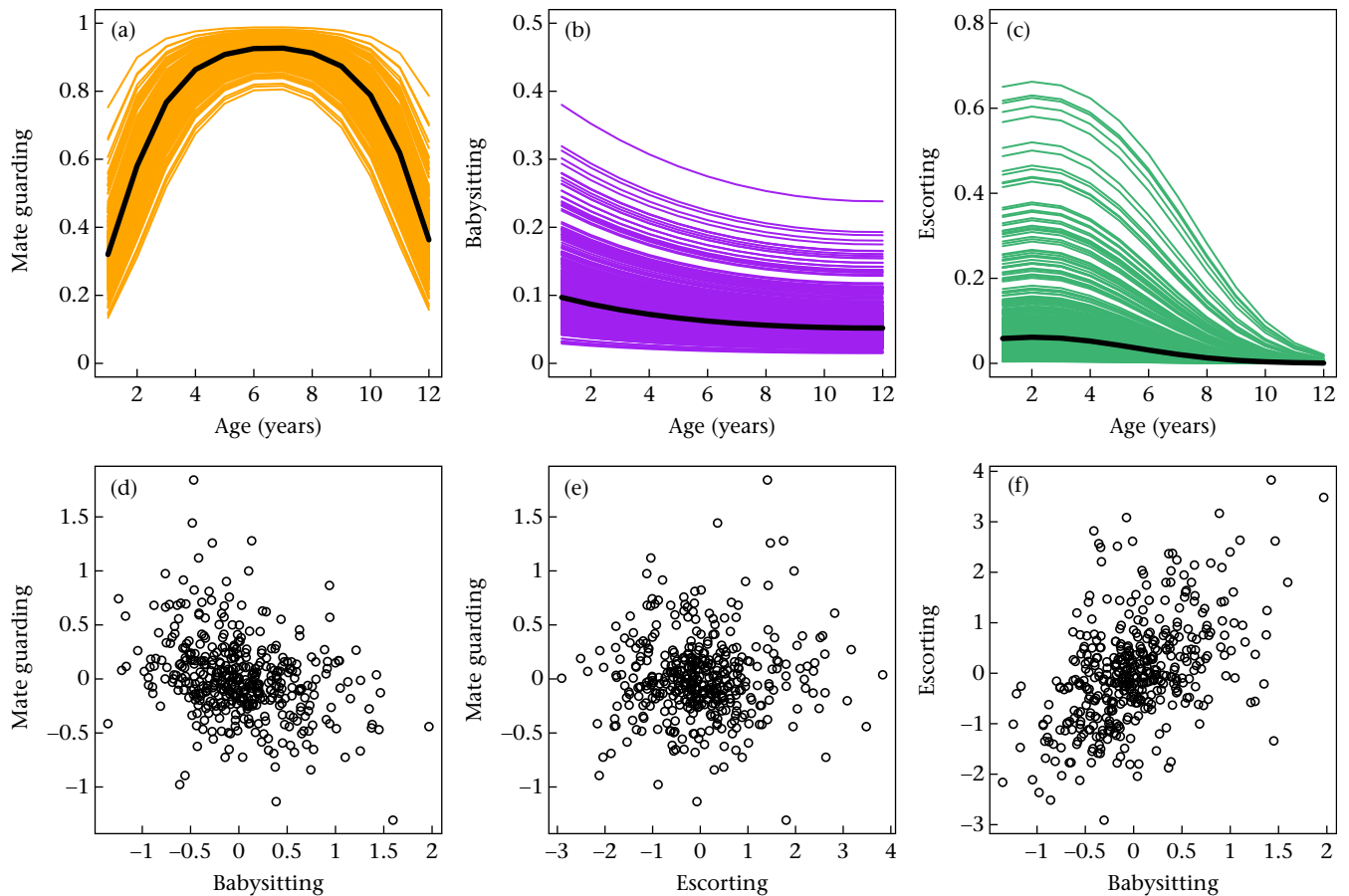


Figure 4. Patterns of individual contributions to (a) mate guarding, (b) babysitting and (c) escorting at different ages and (d–f) visual representations of between-individual covariances between contributions to babysitting, escorting and mate guarding measured over the lifetime of individuals. (a–c) Black and coloured lines show population and individual predicted estimates, respectively, with prediction estimates calculated as posterior modes from an MCMCglmm controlling for variation in group size and the number of females. (d–f) Circles show modes of posterior distributions for each individual's mean estimate of each behavioural trait (from model M2). Note that individual consistency of contributions to a behavioural trait does not mean that individuals behave consistently over their whole lives; rather it means that individuals behave consistently different from the population mean across different contexts, as shown here. A significant between-individual covariance (f) means that these consistent individual differences from the population mean are correlated across different behavioural traits, i.e. individuals that consistently babysit more than expected also consistently escort more than expected and vice versa.

underlying factors, as suggested by the lack of covariance between cooperative and reproductive behaviours found in our study. Clearly, further research is needed to determine the driver(s) of consistent individual differences in cooperative offspring care in this species and others.

Studies investigating consistency of and covariance between behavioural traits over the lifetime of individuals in the wild are rare, presumably because of the difficulties associated with observing behavioural traits over entire lifetimes and/or because of previous limitations in statistical modelling. With recent evidence suggesting that the use of breeding values (or BLUPs) to investigate lifetime correlations between behaviours may give biased results (Hadfield, Wilson, Garant, Sheldon, & Kruuk, 2010, but see Supplementary material 3), behavioural ecologists are now forced to use more complicated (and perhaps daunting) statistical methods such as multivariate statistical methods (as used here) and/or reaction norm approaches (Carter et al., 2014; Nussey, Wilson, & Brommer, 2007) similar to those used more frequently by quantitative geneticists. The publication of guides to such modelling techniques (Araya-Ajoy & Dingemanse, 2014; Dingemanse & Dochtermann, 2013) has proved helpful in developing these techniques and we have included all of the R script used in the current study as Supplementary material in the hope that it might assist future studies of this type. Why individuals vary consistently in their behaviour is still under debate and it may only

be through advanced statistical modelling approaches that we are able to tease apart the drivers of such consistent behavioural variation.

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Supplementary material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2015.06.022>.

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