Consistent individual differences in cooperative behaviour in meerkats (*Suricata suricatta*)

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Abstract

Although recent models for the evolution of personality, using game theory and life-history theory, predict that individuals should differ consistently in their cooperative behaviour, consistent individual differences in cooperative behaviour have rarely been documented. In this study, we used a long-term data set on wild meerkats to quantify the repeatability of two types of cooperative care (babysitting and provisioning) within individuals and examined how repeatability varied across age, sex and status categories. Contributions to babysitting and provisioning were significantly repeatable and positively correlated within individuals, with provisioning more repeatable than babysitting. While repeatability of provisioning was relatively invariant across categories of individuals, repeatability of babysitting increased with age and was higher for subordinates than dominants. These results provide support for theoretical predictions that life-history trade-offs favour the evolution of consistent individual differences in cooperative behaviour and raise questions about why some individuals consistently help more than others across a suite of cooperative behaviours.

Introduction

Although individual variation in cooperation is a striking feature of many animal societies (Komdeur, 2006), the extent to which individuals differ consistently from one another remains poorly understood. While variation may exist as a result of the balance between mutation and weak selection (Santiago, 1998), nonrandom patterns of variation within individuals are suggestive of natural selection (Dall *et al.*, 2004), particularly where the behavioural trait is costly. Two distinct explanations for the evolution of adaptive individual differences in cooperative behaviour may be suggested. First, individual differences in behaviour may arise as a result of trade-offs between the alternative life-history options available to subordinates, who either can remain in their natal group and help or can disperse to breed independently (Emlen, 1982). Variation in conditions experienced during development may result in contrasting life-history strategies (Biro & Stamps, 2008). For example, individuals born in favourable conditions may be more likely to disperse and

breed successfully as adults (e.g. Russell *et al.*, 2007). Such differences in life-history strategies would, in turn, generate consistent individual differences in cooperative behaviour. The second explanation comes from a game theory perspective where, under certain circumstances, there may be advantages to being predictable (Dall *et al.*, 2004). Specific to cooperation, McNamara *et al.* (2009) recently described a model in which individuals could monitor the cooperative tendencies of others, at a cost, and found that such social awareness resulted in the evolutionary stable outcome of consistent individual differences in cooperation.

Although an understanding of the extent and causes of individual differences in behaviour is relevant in the burgeoning fields of phenotypic plasticity (Pigliucci, 2001; Nussey *et al.*, 2007) and animal personality (Sih *et al.*, 2004; Dingemanse & Réale, 2005), few studies of natural populations have yet considered whether individual differences in cooperative behaviour are consistent over time. Detailed studies of cooperative behaviour have instead focused principally on establishing the influence of current ecological and social factors, such as food availability or group size, on contributions to helping (e.g. Legge, 2000; Clutton-Brock *et al.*, 2001). Most empirical work on the individual consistency of

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behaviour has focused on male courtship displays or mating behaviour (e.g. Clark & Moore, 1995; Garamszegi *et al.*, 2006) and female preference for these traits (e.g. Forstmeier & Birkhead, 2004; Holveck & Riebel, 2007). There has been, to our knowledge, no study directly measuring whether cooperative behaviour is consistent. Given that repeatability can set the upper limit to heritability (Boake, 1989; but see Dohm, 2002), investigating the consistency of cooperative behaviour is an important step in understanding the evolution of cooperation.

In this study, we investigate the consistency of individual differences in cooperative behaviour in meerkats (*Suricata suricatta*). The most widely followed approach to quantifying consistency is to measure a repeatability index, or a type of intraclass correlation coefficient (ICC), which gives the proportion of total phenotypic variation that is attributed to variation among individuals (Lessells & Boag, 1987). Formally, this measure of repeatability (*R*) is defined as

$$R = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2} \quad (1)$$

where σ_α^2 is the among-individual variance and σ_ε^2 is the within-individual variance. Traditionally, researchers conducted a one-way ANOVA to measure repeatability (e.g. Clark & Moore, 1995; Freeman-Gallant, 1998), which is a simple and effective technique but limited by its assumptions. Recent developments in statistical modelling have enabled measuring repeatability of traits that do not follow a normal distribution (Browne *et al.*, 2005; Carrasco & Jover, 2005) and, by including fixed effects, random effects or both in such models, it is possible to calculate repeatability while controlling for confounding factors (Nakagawa & Schielzeth, 2010). Such repeatability has been termed 'adjusted repeatability', as the addition of terms in the model influences the values of the variance components (σ_α^2, σ_ε^2 or both) and therefore changes the repeatability value. In addition, 'conditional repeatability' (Nakagawa & Schielzeth, 2010) can be calculated for specific values of fixed-effect terms in the model (for example, sex-specific or age-dependent repeatability). Rather than analysing data subsets separately, this approach allows the calculation of repeatability for specific classes relative to total phenotypic variation (rather than variation of the subset only).

Comparing the conditional repeatability of cooperative behaviour for different types of individuals in a group might support the prediction that repeatability varies between different classes, in relation to variation in the costs of cooperation (Heinsohn & Legge, 1999). Younger individuals, for example, may be less consistent as they are growing and hence more sensitive to food availability, with their behaviour yet to be canalized (Bell *et al.*, 2009). Further reason to predict an age-dependent pattern in repeatability is provided by evidence from

quantitative genetic studies in which heritability of life-history and morphological traits increases with age (Charmantier *et al.*, 2006; Wilson *et al.*, 2007). Second, if the sexes vary in the relative benefits of cooperative behaviour (Hodge, 2007), males and females may exhibit different levels of consistency, with the sex that receives fewer benefits being less constrained in their helping and hence less repeatable. Finally, if breeders incur the costs of reproduction consistently across breeding attempts (Williams, 1966), they are likely to be more repeatable in their cooperative behaviour than helpers who mediate their cooperative effort according to more variable environmental characteristics.

When marked individual differences in behaviour exist, it is important to investigate how they are correlated within individuals across contexts, as exemplified in the study of behavioural syndromes (Sih *et al.*, 2004; Dingemanse & Réale, 2005; Réale *et al.*, 2007). The sign of correlations between cooperative behaviours which act in the same direction may shed light on individual variation in terms of specialization and trade-offs. Negative correlations would suggest that individuals specialize into particular roles, akin to division of labour in insect societies (reviewed in Bourke & Franks, 1995), and also suggest that increased investment in one type of costly helping behaviour may be traded off with investment in other types of helping. Evidence for such specialization has been found in noisy miners (Arnold *et al.*, 2005) and cichlids (Bergmüller & Taborsky, 2007). In contrast, positive correlations would indicate a helping syndrome, whereby individuals are either particularly helpful or selfish (e.g. subordinate female meerkats, Clutton-Brock *et al.*, 2003). This in turn raises the question of why selfish, or less cooperative, individuals are tolerated.

Our long-term study of meerkats provided an unusual opportunity to investigate the consistency of individual differences in cooperative behaviour and how different components of cooperation are correlated. Meerkats are obligately cooperative mongooses living in groups of up to 50 individuals, with a dominant pair monopolizing access to reproduction and subordinates of both sexes assisting in rearing young (Clutton-Brock *et al.*, 2001). Adults provide two primary types of alloparental care: (i) babysitting, where one or more carers remain at the natal burrow to guard the pups while the rest of the group forages throughout the day (when pups are aged 0–20 days) and (ii) provisioning, where adults provide pups with food items when they are old enough to join the foraging group but have yet to develop skills of independent foraging (aged 20–90 days) (Doolan & Macdonald, 1999). Certain categories of individuals contribute to cooperation more than others: dominant individuals tend to do the least helping (Clutton-Brock *et al.*, 2004); females contribute more to both babysitting and provisioning than males (Clutton-Brock *et al.*, 2002); and helping effort changes with age (Clutton-Brock *et al.*,

2002). Furthermore, as mentioned previously, babysitting is positively correlated with provisioning within females (Clutton-Brock *et al.*, 2003). Although there is evidence that individuals compensate for the cost of cooperative behaviour by changing their contribution depending on their effort in the previous breeding season (Russell *et al.*, 2003), no study has yet looked at the extent to which individuals are repeatable in cooperative behaviour over longer timescales, nor whether the degree of repeatability varies according to age, sex or status.

In this study, we used the long-term data set of meerkat cooperative behaviour to investigate the following: first, whether contributions to babysitting and provisioning were repeatable over time; second, whether repeatability varied depending on the type of behaviour in question; third, whether repeatability changed with age and sex-status category and fourth, whether babysitting and provisioning were correlated, and how this correlation varied across age and sex-status categories.

Methods

Measuring cooperative behaviour

To investigate patterns of repeatability in helping behaviour, we focused on cooperative pup care, which is primarily manifested in two behaviours in meerkats: babysitting and provisioning (Doolan & Macdonald, 1999; Clutton-Brock *et al.*, 2001). Analyses were based on per-litter measures of babysitting and provisioning collected between January 1998 and May 2008 from 646 individuals (2–19 measures per individual) rearing 200 litters in 18 groups. Age was classified into three categories: <1 year, 1–2 years and >2 years. This categorization was appropriate to the life history of meerkats: as individuals reach sexual maturity at 7–11 months, those <1 year are still growing; between 1 and 2 years, adults tend to remain in their natal group to help and, beyond 2 years, individuals are more likely to attempt to disperse permanently (Clutton-Brock *et al.*, 2002), with few individuals surviving beyond 4 years of age.

Babysitting
Babysitting was measured as the number of half days an individual remained to babysit a litter of pups in the period from the birth of a litter until the day pups started foraging with the group (around 25–30 days, Clutton-Brock *et al.*, 2003). This was performed on a half-day basis as individuals acting as babysitters often changed between morning and afternoon, particularly if the group returned to the burrow in the middle of the day.

Provisioning
Provisioning was measured as the number of occasions an adult was observed to bring food to a begging pup

during the peak period of provisioning (30–75 days, Brotherton *et al.*, 2001; Young *et al.*, 2005).

Statistical analysis

Statistical analysis was conducted using **R** 2.9.0 (R Development Core Team 2009). We calculated point estimates for repeatability of cooperative behaviour on the original (count) scale by conducting a variance components analysis from a generalized linear mixed model (using the function glmmPQL in the library MASS, Venables & Ripley, 2002), with Poisson error family, as both babysitting and provisioning were count data (Carrasco & Jover, 2005). We used the following formula to estimate repeatability (Carrasco & Jover, 2005; Carrasco, 2009), where R is the count-scale repeatability for count data with multiplicative over-dispersion, $E[Y_{ij}]$ is the observed count for the ith individual at the jth level, ω, σ_α^2 and β_0 are the multiplicative dispersion parameter, the among-individual variance and the grand mean (the intercept and fixed-effect predictors), respectively:

$$R = \frac{E[Y_{ij}] \cdot (\exp(\sigma_\alpha^2) - 1)}{E[Y_{ij}] \cdot (\exp(\sigma_\alpha^2) - 1) + \omega} \tag{2}$$

$$E[Y_{ij}] = \exp\left(\beta_0 + \frac{\sigma_\alpha^2}{2}\right) \tag{3}$$

Overall adjusted repeatabilities (*sensu* Nakagawa & Schielzeth, 2010) for both babysitting and provisioning were calculated from models including the fixed effects of age category, sex and dominance status, in addition to total half days (babysitting model) and observation time (provisioning model), as these varied among breeding attempts (half days: mean 42.5 half days, range: 20–82; observation time: mean 44.45 h, range: 11.57–105.80 h). As repeatability depends on the grand mean of the model (β_0), and consequently on the scaling of all the fixed effects (Nakagawa & Schielzeth, 2010), we used the mean levels of each fixed-effect coefficient when calculating overall repeatability. In addition, we measured conditional repeatability (Nakagawa & Schielzeth, 2010) for a particular factor (e.g. age category), by setting all other factors to the mean and then calculating the variance components for separate models for each level of the factor of interest (e.g. 1 year, 1–2 years and >2 years). We calculated standard errors and 95 per cent confidence intervals (CI) for repeatability using the Fisher's Z method (McGraw & Wong, 1996). Although the number of breeding attempts varied per individual, we were not concerned that this would affect repeatability as mixed models account for variation in uncertainty created by unbalanced sample sizes (Gelman & Hill, 2007), and a recent meta-analysis demonstrated that repeatability does not vary with the number of observations per individual (Bell *et al.*, 2009).

We compared overall repeatabilities of babysitting and provisioning following the approach of Garamszegi (2006) and Nakagawa *et al.* (2007), conducting a linear mixed model with *Z*-transformed repeatability as the response term, behavioural type (babysitting or provisioning) as a fixed effect and age or sex-status category as a random grouping factor.

To compare repeatability estimates, we followed the approach of comparing effect sizes and 95 per cent confidence intervals rather than basing inferences on *P*-values (Nakagawa, 2004; Garamszegi, 2006; Nakagawa & Cuthill, 2007). Accordingly, we compared the conditional repeatability estimates for babysitting (which were more variable than those for provisioning) by calculating pairwise differences in *Z*-transformed repeatability estimates and asked whether the confidence intervals overlapped with zero.

To investigate the extent to which babysitting was correlated with provisioning, we divided the data set according to the three age (<1 year, 1–2 years and >2 years) and four sex-status (subordinate female, subordinate male, dominant female and dominant male) categories. For each subset, we calculated mean values of babysitting and provisioning for each individual, both Box-Cox transformed for normality, and conducted a Spearman's rank correlation test. To compare whether the strength of the correlation varied across different age or sex-status categories, we compared these seven different correlations by calculating pairwise *Z*-transformed differences and associated confidence intervals as described previously.

Results

Individuals were significantly repeatable both in babysitting and in provisioning (babysitting, $R = 0.218$, 95% CI: 0.126 to 0.305, $P < 0.0001$; provisioning, $R = 0.513$, 95% CI: 0.473 to 0.551, $P < 0.0001$; Table 1). Provisioning was more repeatable than babysitting (LMM: $t_6 = 9.873$, $P = 0.0001$). In addition, whereas the repeatability of provisioning was relatively invariant across different categories of age or status (Table 2, Fig. 1), there was more variation in babysitting (Table 2, Fig. 1). We compared differences in the point estimates and standard errors for repeatability of babysitting among age and sex-status categories (Fig. 2, Table 2). We found that repeatability for individuals >2 years old was higher than for individuals <1 year and 1–2 years old. Dominant individuals of both sexes had lower repeatabilities than subordinates, and there were no differences between males and females in repeatability.

Babysitting and provisioning were positively correlated (Spearman's $r = 0.225$, 95% CI: 0.151 to 0.297, $t_{644} = 5.871$, $P < 0.0001$), although the strength of the correlation varied when we considered subsets of the data separately (Table 3). Nevertheless, when we compared differences in the point estimates for the correlations and their associated standard errors, there were no significant differences in the strength of the correlation across categories (difference in *Z*-transformed *r*: 0.052–0.226, lower 95% CI: −0.261 to −0.018, upper 95% CI: 0.177 to 0.690).

Discussion

Both babysitting and provisioning were significantly repeatable within individuals. In a recent meta-analysis, the mean repeatability of a range of behaviours across

Table 1 Repeatability estimates for babysitting and provisioning, with a breakdown of the values for the numerator and denominator from eqn 2 and the difference in these two values; which correspond to among-individual variance, total variance and within-individual variance, respectively.

	R (SE)	Numerator ($\approx \sigma_\alpha^2$)	Denominator ($\approx$total variance)	Difference ($\approx \sigma_\epsilon^2$)
Babysitting	0.218 (0.046)	0.797	3.66	2.87
Provisioning	0.513 (0.020)	7.22	14.1	6.86

Table 2 Repeatability estimates across categories for both babysitting and provisioning. Categories are abbreviated as follows: SF = subordinate female; SM = subordinate male; DF = dominant female; DM = dominant male. Shown are the repeatabilities and standard errors (see text for details), the associated *P*-value and the number of observations, n(o), and individuals, n(i) used for the calculation of each estimate.

	Babysitting			Provisioning		
	R (SE)	P	n(o), n(i)	R (SE)	P	n(o), n(i)
Age						
<1 year	0.166 (0.056)	0.005	896, 562	0.510 (0.039)	<0.0001	896, 562
1–2 year	0.221 (0.047)	<0.0001	948, 521	0.513 (0.035)	<0.0001	948, 521
>2 year	0.288 (0.042)	<0.0001	738, 250	0.513 (0.036)	<0.0001	738, 250
Category						
SF	0.288 (0.035)	<0.0001	1013, 307	0.534 (0.030)	<0.0001	1015, 307
SM	0.255 (0.031)	<0.0001	1225, 331	0.499 (0.029)	<0.0001	1226, 331
DF	0.045 (0.058)	0.415	185, 34	0.533 (0.079)	<0.0001	183, 34
DM	0.039 (0.077)	0.613	159, 46	0.498 (0.081)	<0.0001	158, 46
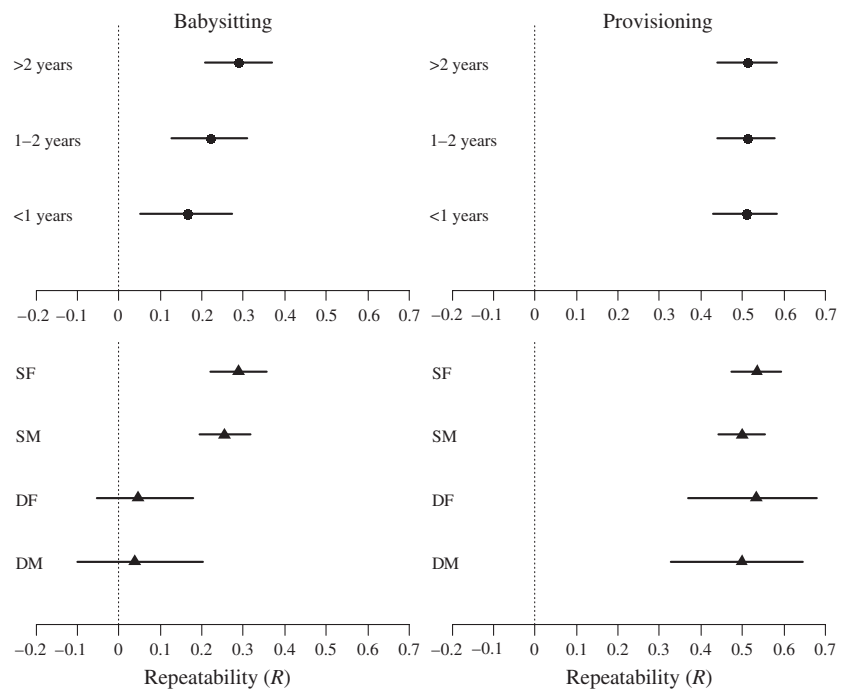
Fig. 1 Repeatabilities and 95% confidence intervals for both babysitting and provisioning across all categories of individual. Those estimates whose confidence intervals do not cross the dotted line at 0 are significantly repeatable at the α = 0.05 level.
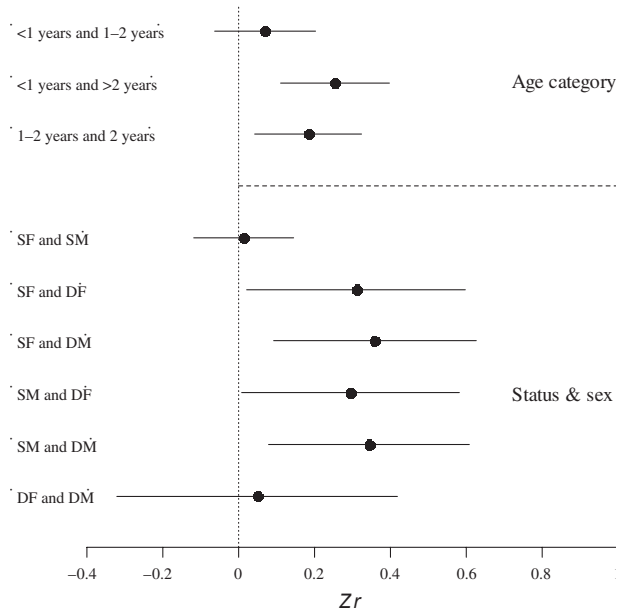
Fig. 2 Differences in point estimates of repeatabilities and 95% confidence intervals of the difference for seven categories of individual for babysitting only. Those differences whose 95% confidence interval does not cross the dotted line are significantly different at the α = 0.05 level.

Table 3 Results from Spearman's rank correlation tests, including r_S estimates and associated 95% confidence intervals, to investigate the association between babysitting and provisioning both in general and for the seven different subsets of data.

	r_S estimate (CI)	t	df	P
All	0.225 (0.151/0.297)	5.871	644	<0.0001
<1 year	0.241 (0.162/0.318)	5.882	560	<0.0001
1–2 year	0.294 (0.214/0.371)	7.012	518	<0.0001
>2 year	0.168 (0.045/0.286)	2.681	248	0.008
SF	0.190 (0.080/0.296)	3.381	305	0.001
SM	0.240 (0.135/0.339)	4.477	329	<0.0001
DF	0.084 (−0.261/0.411)	0.479	32	0.635
DM	0.301 (0.008/0.546)	2.069	43	0.045

babysitting ($R = 0.22$). Given that repeatability may indicate the upper limit of heritability (Boake, 1989; Hayes & Jenkins, 1997; but see Dohm, 2002), a fruitful avenue for future research would be to investigate whether cooperative behaviour is heritable in this species, as in western bluebirds (Charmantier et al., 2007), and for provisioning effort of parents in cooperatively breeding long-tailed tits (MacColl & Hatchwell, 2003).

Previous work on meerkats demonstrated that helping is condition dependent and individuals mediate the costs of helping by adjusting their contributions according to how much they helped in the previous breeding attempt (Russell et al., 2003). Our analysis, based on a 10-year timescale (covering the lifespan of >95 percent of all individuals, Sharp & Clutton-Brock, 2010), shows, that

several taxa was 0.37 (Bell et al., 2009), so our results indicate that meerkats are highly repeatable in feeding young ($R = 0.51$) and below average in repeatability of

despite short-term compensation, individuals remain consistently different from one another in their cooperative behaviour in the long term. While within-individual consistency may be explained by high mutation rates and weak selection (Santiago, 1998), the costly nature of cooperative behaviour suggests that consistent individual differences here are adaptive. Our results may be explained in the light of the hypothesis that variation in life-history strategies mediates consistent individual differences in cooperation (Dall *et al.*, 2004; Stamps, 2007; Wolf *et al.*, 2007), with strategies determined through initial individual differences in physiology or morphology, such as growth rates (Biro & Stamps, 2008). Life-history strategies are likely to be important in meerkats, where early body weight is predictive of an individual's chance of attaining dominance (Russell *et al.*, 2007), and there is a trade-off between helping and breeding (Young *et al.*, 2005). The alternative explanation that variation in social awareness results in consistent individual differences in cooperation (McNamara *et al.*, 2009) is less likely to explain cooperative pup care in meerkats, as this is a more complex situation than a repeated game between two matched players.

Individuals were more repeatable in their provisioning than babysitting. Before discussing this result, however, it is important to note that, as repeatability estimates depend on the fixed effects included in the model, comparisons from different models should be made with caution (for a similar point about heritability, see Wilson, 2008). With this caveat in mind, we may still gain biological insight from comparing repeatability qualitatively. Repeatability is a ratio (eqn 1), and differences in repeatability may arise as a result either of variations in the numerator (among-individual variation) or the denominator (total variation: within- and among-individual variation combined). Among-individual variance relative to within-individual variance was higher for provisioning than babysitting (Table 1), possibly because of the different timescales on which decisions to babysit or feed pups were made. During the babysitting period, babysitters tended to remain with pups for at least half a day and often an entire day, and hence babysitting was decided on a per-day basis (Clutton-Brock *et al.*, 1998). In contrast, during the provisioning period, all adults were exposed to the stimulus of vocal begging from pups (Doolan & Macdonald, 1999), and hence the decision of whether or not to feed pups was made every time a food item was found. Moreover, the high repeatability of provisioning indicates that most individuals were relatively invariant in this behaviour over their lifetime and, consequently, it is not surprising that there was little variation across categories in repeatability estimates.

Repeatability of babysitting increased with age and was higher for subordinates than dominants. As helping may incur energy costs (Heinsohn & Legge, 1999), the reduced cooperative behaviour observed in both younger individuals (Clutton-Brock *et al.*, 2002) and dominant individuals (Clutton-Brock *et al.*, 2004) may be a result of the trade-off with growth and maintaining dominance, respectively. Reduced mean levels of cooperation are associated with reduced among-individual variation in younger individuals and dominants. As discussed earlier, age and dominance differences in repeatability may be explained by the fact that repeatability is the ratio of among-individual variation compared to total phenotypic variation: if among-individual variation is low, as is the case for both dominant and younger individuals' babysitting, then repeatability, in turn, is low.

There was little evidence for sex differences in repeatability for either babysitting or provisioning. In their recent meta-analysis, Bell *et al.* (2009) found a general pattern for sex differences in repeatability and, specific to offspring care, males are more repeatable than females in their provisioning effort in house sparrows (Schwagmeyer & Mock, 2003; Nakagawa *et al.*, 2007) and long-tailed tits (MacColl & Hatchwell, 2003). We had predicted sex differences in repeatability of babysitting and provisioning in meerkats, as there are striking sex differences in cooperative behaviour (Clutton-Brock *et al.*, 2002). The absence of sex differences in repeatability serves as a reminder that, even if the mean levels of behaviour vary, the variability within individuals may not be different and indicates that similar constraints act on males and females in determining the flexibility of their behaviour.

In line with a previous study (Clutton-Brock *et al.*, 2003), we found that babysitting and provisioning were positively correlated within individuals, with the strength of the correlation relatively invariant across different categories, apart from a tendency to decrease with age. Demonstrating repeatability across time and correlations across contexts suggests a helping syndrome, with different behavioural types for particularly cooperative or selfish individuals. Our results are in contrast to other similar investigations into cooperative breeders, in which negative correlations between cooperative activities have been found (Arnold *et al.*, 2005; Bergmüller & Taborsky, 2007). Although we have focused on cooperative behaviours related to the care of young, future work will investigate correlations across other types of behaviour, including those in functionally different contexts, including exploration and aggression. The existence of different helping types within a group sets the stage for further investigation into why certain individuals display particularly elevated cooperative behaviour and why less helpful individuals are tolerated.

To conclude, we have provided a rare demonstration that cooperative care of young is significantly repeatable within individuals, by considering two types of cooperative behaviour in a wild mammal. In spite of the fact that cooperative behaviour may be sensitive to current social and ecological conditions, such as group size or food availability (Legge, 2000; Clutton-Brock *et al.*, 2001), our results imply that individuals remain relatively consistent in their cooperative effort over time.

Recent theory suggests that differences in underlying state variables, such as body size or growth rate, coupled with life-history trade-offs can result in the evolution of consistent individual differences (Dall *et al.*, 2004; Stamps, 2007). In cooperative breeders, individuals may follow particular life-history strategies because of the trade-off between helping and breeding combined with intrinsic individual differences in body size. Further work investigating the repeatability of traits such as growth rate and foraging efficiency would help elucidate the mechanisms by which such trajectories are established.

Acknowledgments

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