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Nichols, Hazel J.

2021-09

Nichols , H J , Arbuckle , K , Sanderson , J L , Vitikainen , E I K , Marshall , H H , Thompson , F J , Cant , M A & Wells , D A 2021 , ' A double pedigree reveals genetic but not cultural inheritance of cooperative personalities in wild banded mongooses ' , Ecology Letters , vol. 24 , no. 9 , pp. 1966-1975 . <https://doi.org/10.1111/ele.13833>

<http://hdl.handle.net/10138/333405>

<https://doi.org/10.1111/ele.13833>

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LETTER

A double pedigree reveals genetic but not cultural inheritance of cooperative personalities in wild banded mongooses

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Funding information

This work was supported by Natural Environment Research Council (NERC) Standard Grants (NE/J010278/1, NE/S000046/1 and NE/N011171/1) and European Research Council Starting Grant (SOCODEV, grant number 309249) awarded to M.A.C., a Leverhulme International Fellowship (IAF-2018-006) awarded to H.J.N., and a Humboldt Research Fellowship for Experienced Researchers awarded by the Alexander von Humboldt Foundation to H.J.N.

Editor: Minus van Baalen

Abstract

Personality traits, such as the propensity to cooperate, are often inherited from parents to offspring, but the pathway of inheritance is unclear. Traits could be inherited via genetic or parental effects, or culturally via social learning from role models. However, these pathways are difficult to disentangle in natural systems as parents are usually the source of all of these effects. Here, we exploit natural 'cross fostering' in wild banded mongooses to investigate the inheritance of cooperative behaviour. Our analysis of 800 adult helpers over 21 years showed low but significant genetic heritability of cooperative personalities in males but not females. Cross fostering revealed little evidence of cultural heritability: offspring reared by particularly cooperative helpers did not become more cooperative themselves. Our results demonstrate that cooperative personalities are not always highly heritable in wild, and that the basis of behavioural traits can vary within a species (here, by sex).

KEYWORDS

cooperation, cultural inheritance, helping syndromes, heritability, missing inheritance, personality

INTRODUCTION

Cooperation between organisms is key to the evolution of complex societies (Cornwallis et al., 2010), but understanding how cooperation can evolve and be maintained in the face of selfish behaviour is a long-standing problem in biology (Riolo et al., 2001). Indeed, among social animals, individuals often demonstrate profound differences in the degree to which they cooperate (Komdeur, 2006), which could generate substantial fitness differences between cooperative and non-cooperative phenotypes. Some variation in the propensity to cooperate can be explained by characteristics that affect the fitness costs and benefits of cooperating, such as age (Hill & Hurtado, 2009), energetic state (Wright et al., 2001), relatedness (Reyer, 1984; Russell & Hatchwell, 2001) and sex (Clutton-Brock et al., 2002; Hodge, 2007). Therefore, variation in cooperation is usually interpreted as adaptive plasticity. However, even after these factors have been taken into account, considerable variation between individuals usually remains, and animals often show within-individual repeatability in their propensity to cooperate across time and in different contexts (Bergmüller et al., 2010). In these cases, cooperation can be considered a personality trait or ‘helping syndrome’ (English et al., 2010). Such traits are important from an evolutionary perspective, having profound effects on direct and indirect fitness (Smith & Blumstein, 2008; Wolf & Weissing, 2012).

Despite progress in identifying helping syndromes, we have a very limited understanding of their basis (Kasper et al., 2017b). Studies of wild cooperatively breeding birds suggest that the propensity to cooperate is highly heritable (Charmantier et al., 2007; Wang & Lu, 2018), raising the possibility that cooperative phenotypes might be under genetic control. However, other inheritance pathways (not taken into account in these studies) may also have a strong influence on helping syndromes (Engelhardt et al., 2018). The ‘inclusive heritability’ discovered in previous studies may therefore derive from both genetically and non-genetically inherited information (Danchin & Wagner, 2010). For example, variation in cooperative behaviour can arise from maternal or paternal effects, whereby the phenotype or genotype of parents directly impacts on offspring phenotype, independently of the genes that the offspring inherits (Kasper et al., 2017a).

Personality differences may also show cultural heritability, whereby traits are transmitted via social learning from role-models (Danchin & Wagner, 2010). This can lead to phenotypic variation that is heritable without requiring any genetic component, and may even provide a non-genetic ‘second inheritance system’ (Sheppard et al., 2018; Whiten, 2005, 2017; Whiten et al., 2017). In theory, cooperation can spread rapidly even among non-relatives via generalised reciprocity, that is, a rule to help others if helped by others (Van Doorn & Taborsky, 2012;

Rankin & Taborsky, 2009). While cultural influences on cooperation are apparent in humans (Boyd & Richerson, 2009; Stanca, 2009) and in some lab and domestic animals (Gfrerer & Taborsky, 2017; Leimgruber et al., 2014; Rutte & Taborsky, 2007) the cultural inheritance of cooperative traits in natural populations has been little explored.

A major barrier to understanding the relative importance of social and genetic effects on helping syndromes, and indeed many other behavioural traits, is the difficulty in detangling these factors (Danchin, 2013; Danchin et al., 2011; Danchin & Wagner, 2010). In most natural situations, the genetic parents have a substantial social influence on young, presenting a major challenge to differentiate between alternative inheritance routes. This is likely to be the predominant reason for the dearth of studies on the subject, with only a handful investigating the inclusive heritability of cooperation, none of which attempt to decompose this into genetic and non-genetic components (Koenig & Dickinson, 2016). One potential solution is to experimentally separate genetic and social factors using cross-fostering, whereby offspring are removed from their genetic parents and are raised by unrelated ‘foster’ parents (Danchin et al., 2011). However, this is rarely feasible, particularly for wild mammals where birth dates cannot be controlled and opportunities to manipulate litters are limited.

Here, we take advantage of natural ‘cross-fostering’ in wild banded mongooses, *Mungos mungo*, to investigate sources of variation in cooperative behaviour. Banded mongooses are small (<2 kg) cooperatively breeding African mammals that live in mixed sex groups of 10–30 individuals (Cant et al., 2013). Unlike most cooperative breeders (Lukas & Clutton-Brock, 2012), they do not have a single dominant pair and several females in each group (median = 3 females, range 1–13) breed together up to four times per year (Cant et al., 2016). Within each group, breeding is tightly synchronised, with females usually giving birth on the same night (Hodge et al., 2011). Individual litters are combined immediately after birth and are raised communally, by parents and allo-parents (Cant et al., 2016).

Adults direct two main forms of care towards pups; babysitting and escorting, shown in Figure 1 and described in detail in Cant et al., (2016). For the first ~30 days, the young remain in the communal den while the group forages several hundred meters away. One or more ‘babysitters’ forego foraging to remain at the den and defend the pups from predators and rival groups. Once the pups are able to forage with the group, each pup forms a one-to-one association with an adult carer termed an ‘escort’, who feeds, grooms, carries and protects the pup until nutritional independence at 90 days. Critically, relatedness has little impact on patterns of helping behaviour and pups are no more closely related to their escorts than to random group members (mean relatedness within pup-adult pairs is 0.21; substantially

(a)



babysitters help a litter of pups



(b)



escorts provide one-to-one care



FIGURE 1 The two forms of pup care shown by banded mongooses: a) babysitting and b) escorting. Babysitting involves one or more individuals remaining at the den to protect young pups (aged <30 days) whilst the rest of the group forages and escorting involves a one-to-one relationship between an adult and pup (aged 30–90 days), whereby they remain in close proximity and the adult feeds, grooms, carries and protects the pup. Critically, pups are no more closely related to their escorts than to random group members. Escorting therefore creates a natural ‘cross fostering’ experiment to decouple routes for genetic and cultural inheritance

lower than that between parent–offspring pairs) (Vitikainen et al., 2017). Escorting therefore decouples routes for genetic and non-genetic inheritance, making the banded mongoose an ideal system to disentangle the impact of genes, culture, parental effects and early life conditions on phenotype (Sheppard et al., 2018).

Previous studies have shown that escorts act as role-models for their pups, passing down foraging techniques (Müller & Cant, 2010) and lifelong foraging niches (Sheppard et al., 2018), thus demonstrating the potential for cultural inheritance. Furthermore, helping syndromes have been described in this species: Sanderson et al., (2015a) found that male contributions to babysitting and escorting are repeatable across the lifetime (babysitting; $R_{\text{logitA}} = 0.12$, escorting; $R_{\text{logitA}} = 0.25$) and are significantly correlated with each other ($R\text{-COV}_{\text{BS-ESC}} = 0.38$). This system therefore provides an excellent opportunity to investigate genetic and cultural influences on cooperative behaviour in the wild.

Here, we use a 21-year dataset on contributions to helping behaviour in 800 adult wild banded mongooses across 17 social groups, to investigate the basis of helping syndromes in this species. Specifically, we assess cultural and genetic inheritance of variation in contributions to cooperation through using the ‘double-pedigree’ approach (Danchin et al., 2013), incorporating a genetic pedigree based on parentage assignment and a cultural pedigree based on observed escorting relationships. We also investigate the impact of early life conditions by incorporating maternal, paternal and escort effects, and the impact of the permanent and current social environments and ecological conditions.

MATERIALS AND METHODS

Study site and data collection

Behavioural, genetic and life-history data were collected between 1995 and 2016 as part of an ongoing long-term study of wild banded mongooses in Queen Elizabeth National Park, Uganda (0°12’S, 29°54’E). The study site comprises approximately 10km² of savannah which is home to around 200 individual banded mongooses at any one time, divided into 8–12 social groups (Cant et al., 2016). The climate is equatorial, with little seasonal fluctuation in temperature or day length. Annual precipitation is typically 800–900 mm, with two dry periods in January–February and June–July (Cant, 2000). Increasing rainfall increases the abundance of the small invertebrate prey that banded mongooses feed on (Marshall et al., 2017) and influences patterns of helping behaviour (Nichols et al., 2012). Rainfall data are collected from Mweya Meteorological Station at the centre of the study site.

One or two adults in each group are fitted with a 26 g radio collar (<2% of body mass) with a 20 cm whip antenna, which allows groups to be located. All individuals in the population can be identified on sight because of a unique fur shave or dye pattern or colour-coded plastic collar. These markings are maintained by trapping all individuals in the population every 3–6 months as described in previous publications (Cant, 2000; Hodge, 2007; Jordan et al., 2010).

Behavioural observations of care

Groups are habituated to human observation (within 5 m) and are visited every 1–3 days to collect detailed behavioural and life history data. When groups have dependent young, behavioural observations of babysitting and escorting are made. Babysitters are identified by either being observed at the den while the rest of the group forages at least 100m away, or by their absence from the group on foraging trips. This method has been verified by a previous study (Cant, 2003) and is effective because banded mongooses very rarely leave their social group on short-term forays (Hodge, 2007). Escorting is a conspicuous behaviour and is easily identified in the field using behavioural scans; adults that are within 30cm of a particular pup for more than 50% of scans for an observation period were classed as escorts. Observation periods last at least 20 min and are carried out during morning and/or afternoon foraging sessions. Adults vary in the amount of escorting care they provide, and many adults do not escort a pup. Further information on escorting, including videos, can be found in Sheppard et al., (2018) and Wells et al., (2020).

Cultural pedigree

A cultural pedigree was constructed using escorting relationship data. Each individual's escort was listed as its 'dam' while no 'sire' was assigned. Approximately, 70% of banded mongoose pups have a single escort while the remainder sequentially associate with different adults during the escorting period (Sheppard et al., 2018). When pups were observed with multiple adults, we assigned the adult that escorted the pup most frequently, and on a minimum of two occasions, as its primary escort (dam). A previous study found that the primary escort has a substantial influence over social traits such as foraging niche, even when the pup sometimes associated with other adults (Sheppard et al., 2018). In some cases, it was not possible to determine the primary escort, either because of a lack of behavioural data (for example if the individual immigrated into the population as an adult), because two adults escorted the pup same number of times, or because the pup had no escort. In these cases, we did not assign an escort to the individual. Our cultural pedigree comprised of 279 escorts assigned to 672 pups and was up to seven generations deep (median = 2, Q1 = 1, Q3 = 2). The number of pups assigned to each escort over its lifetime ranged from 1 to 14, with a median of 2.

Genetic pedigree

Because of birth synchrony and communal care, the parentage of pups could not be determined behaviourally,

so genetic parentage assignment was required. The first time individuals were captured, they were anaesthetised and fitted with a PIT tag (TAG-P-122IJ, Wyre Micro Design) for permanent identification and their sex was determined through visual inspection. A 2 mm tissue sample was taken from the tail tip using surgical scissors and a dilute solution of potassium permanganate was applied to minimise infection risk. DNA was extracted and samples were genotyped for 35–43 microsatellite loci (Sanderson et al., 2015b; Wells et al., 2018).

Parentage was determined using the programs MASTERBAYES (Hadfield et al., 2006) and COLONY (Jones & Wang, 2010). MASTERBAYES was used as the primary parentage assignment program because it can incorporate phenotypic data, which can result in larger numbers of higher confidence assignments. COLONY was used to confirm the MASTERBAYES assignments and to assign sibships among individuals with one or both unsampled parents. The latter provides putative information about the relationships among founders and immigrants rather than assuming that they are unrelated. Full details of genotyping and pedigree construction, including datasets, parameter values and R code are provided in Sanderson et al., (2015b) and Wells et al., (2018). The pedigree includes 1912 individuals with 1725 assigned mothers and 1625 assigned fathers and 777 individuals with all four grandparents assigned. The genetic pedigree is up to nine generations deep (median = 3, Q1 = 1, Q3 = 5).

Ethical statement

Our research is carried out under license from the Uganda National Council for Science and Technology, and all procedures have been approved by the Uganda Wildlife Authority. All research procedures adhere to the ASAB Guidelines for the Treatment of Animals in Behavioral Research and Teaching and have been approved by the Ethical Review Committee of the University of Exeter. Our trapping procedure has been used over 8000 times, and tissue samples have been taken from over 2000 individuals with no adverse effects.

Statistical analysis

We confirmed the existence of significant repeatability in helping behaviour and the positive association between the two forms of help (babysitting and escorting), which were previously demonstrated by Sanderson et al., (2015a) using a smaller dataset; see the Supplementary Information, Tables S1 and S2 for details.

We assessed genetic and non-genetic sources of variation in contributions to cooperation. Analyses were conducted in R using 'animal models' run in the package MCMCglmm (Hadfield, 2010). Animal models usually

contain a single pedigree based on parentage data. However, to analyse genetic and cultural influences on behaviour simultaneously, we used the 'double pedigree' approach developed by Danchin et al., (2013). Our models therefore incorporated two pedigrees, the genetic pedigree and the cultural pedigree. The degree of overlap between the two pedigrees was low; only 4.75% of the individuals used in our models (and which had known parents and primary escorts) were escorted by their mother, and a further 5.55% were escorted by their father. We also incorporated other non-genetic sources of variation as random effects; the identity of the individual (potential helper) along with the identity of its mother, father and escort, the social group that the potential helper was present in, and the identity of the communal litter that helping was being directed towards.

We constructed eight models (detailed in Table S3), each including a measure of cooperative behaviour as the response variable, fixed effect explanatory variables that have been shown in previous studies to be associated with helping behaviour (defined in Table S4), and random effects (defined in Table S5) that may explain variance in helping behaviours.

Previous studies of banded mongooses have demonstrated fundamental differences between the sexes in the factors that influence helping behaviour (Hodge, 2007; Nichols et al., 2012). We therefore constructed separate models for males and females. It is possible that different factors influence the propensity of an individual to help and influence the quantity of help provided. We therefore constructed separate models to investigate (1) whether or not a given individual provided help to a given litter (their propensity to help) and (2) for those individuals that did help, how much help they provided (time spent helping). The significance of random effects was determined through inspecting the posterior distributions (shown in the supplementary information); we deemed a variable to explain significant variance in helping behaviour if the lower 95% CI of its posterior estimate was ≥ 0.001 , which occurred when the posterior distribution was not truncated at zero.

Binary response variables (addressing whether an individual contributed to care) were modelled with a categorical family. To avoid poor mixing, the random effects for individual, genetic pedigree and cultural pedigree were fitted using a parameter-expanded prior $V = 1$, $\nu = 0.002$, $\alpha \cdot \mu = 0$ and $\alpha \cdot V = 1000$ following Hadfield (2010). The remaining random effects and all fixed effects were fitted using inverse-gamma priors $V = 1$ and $\nu = 0.002$. These all represented weak priors that ensured that the information from the model overwhelmingly came from the data. The residual unit variance was fixed to 1 by convention because it is not calculable in a binary model as there is only a single realisation of each data point. Binary models were run for 1,300,000 iterations with a burnin of 5000 and a thinning interval of 1000.

Models investigating how much help was provided by those individuals that did help were modelled with a binomial family. As with the binary models, all of our priors were weak; the random effects for individual, genetic pedigree and cultural pedigree were fitted using a parameter-expanded prior $V = 1$, $\nu = 0.002$, $\alpha \cdot \mu = 0$ and $\alpha \cdot V = 1000$ while the remaining random effects and all fixed effects were fitted using inverse-gamma priors $V = 1$ and $\nu = 0.002$. To avoid autocorrelation, binomial models were run for 6,500,000 iterations with a burnin of 10,000 and a thinning interval of 5000.

We checked model outputs for autocorrelation and effective sample sizes (all above 900), which indicated good sampling of the posterior distribution. Posterior distributions of the parameters (Figure S1) strongly suggested that the data were sufficiently informative for effective inference. The proportion of variance explained by random effects was calculated following Nakagawa and Schielzeth (2010) for models using a logit link with additive overdispersion.

RESULTS

The full outputs of our eight models are shown in Table S3 and the modal variances explained by each of our random effects are visualised in Figure 2. We found significant genetic heritability (h^2) of babysitting and escorting behaviour in male banded mongooses. The modal genetic heritabilities of the propensity of males to engage in babysitting and escorting were 7.0% (95%CI: 1.1, 13.8) and 15.2% (95%CI: 4.1, 28.7), respectively. However, for males that contributed to helping, there was no significant genetic heritability in the amount of time spent escorting and babysitting. In contrast with patterns found in males, females showed no significant genetic heritability in any form of helping behaviour (modal variances $< 1\%$).

We found little evidence of cultural heritability of helping behaviour; the cultural pedigree explained a mode of $\leq 0.1\%$ variance in helping behaviour in all models except for the amount of time males spent babysitting, where it explained 2.4% of variance, but this was not significantly greater than zero (95% CI: 0.0, 4.3; Figure S1). This suggests that neither the propensity to help nor the amount of time spent helping is culturally inherited via the escort.

The identity of the social group of the potential helper had little impact on helping behaviour, explaining a mode of 3.2% (95% CI: 0.7, 13.6) of variance in the contributions of female helpers to babysitting, and no significant variance in any other model ($< 1\%$ variance). This suggests that differences in group-specific factors such as culture or territory quality do not promote a situation whereby some groups are more 'helpful' than others.

Once genetic heritability had been accounted for, individual identity did not explain significant variance

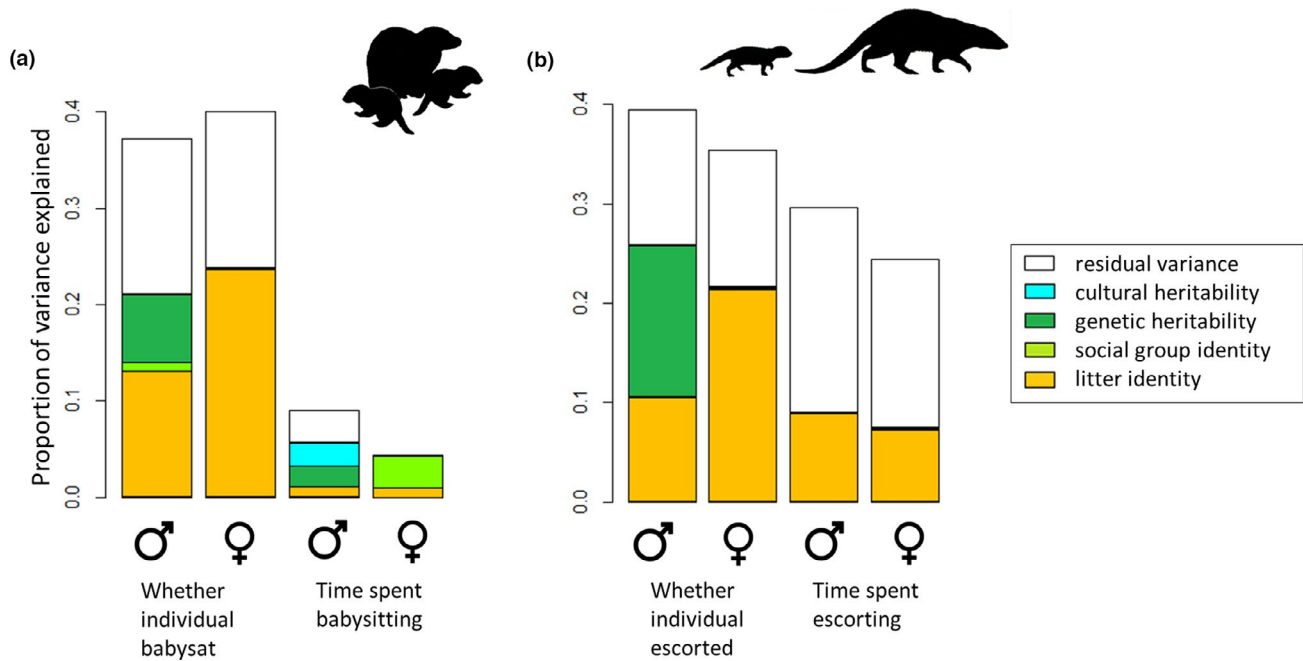


FIGURE 2 The proportion of variance explained by the random factors included in models of (a) babysitting and (b) escorting. For each communal litter, we modelled whether adult group-members contributed to babysitting or escorting the pups and, for those individuals that did contribute to helping, we modelled the proportion of observation sessions on which they helped (time spent babysitting or escorting). Note that the variance explained by the identity of the individual, mother, father and escort is too small to be visible in the figure

in helping behaviour in any of our models (explaining a mode of <0.1% variance). Similarly, we did not find a significant impact of the identity of the individual's mother, father or escort on subsequent helping behaviour (explaining a mode of <0.3% variance in all models) implying that early life effects that could result from consistent differences between mothers, fathers and escorts do not impact life-long helping behaviour.

Significant variance in helping behaviour was explained by the identity of the communal litter of pups being raised in almost all of our models. Litter identity explained a mode of 13.1% (95% CI: 9.2, 17.3) and 23.6% (95% CI: 17.5, 29.9) of variation in the propensity of males and females to babysit and 10.4% (95% CI: 5.5, 16.5) and 21.3% (95% CI: 11.9, 32.7) of variation in the propensity of males and females to escort. It also explained 1.1% (95% CI: 0.6, 1.9) and 1.0% (95% CI: 0.2, 2.1) of variation in the amount of time males and females spent babysitting and 8.8% (95% CI: 5.0, 15.1) of variation in the amount of time males spent escorting, however, it did not explain significant variance in the amount of time females spent escorting (mode = 7.2%, 95% CI: 0.0, 15.3). Note that variance explained by litter identity is after accounting for fixed effects relating to current conditions (group size, litter size, rainfall and parentage), which also affect helping behaviour. The impact of litter identity is therefore likely to result from further factors relating to the current physical, physiological and social environment that we were unable to measure during our study.

DISCUSSION

We used genetic and cultural pedigrees, along with behavioural, demographic and environmental data, to investigate factors underlying helpful personalities in wild banded mongooses. We found significant genetic heritability of babysitting and escorting behaviour in males, but not females. In contrast, we found little evidence for cultural heritability of helping behaviour in either sex.

Significant but low genetic heritability of helping behaviour of males

Our findings suggest that the helping syndromes previously found in male banded mongooses (Sanderson et al., 2015a) have a heritable genetic basis. Heritability was relatively low in comparison to that found in the handful of other studies of wild cooperative breeders. For example, Charmantier et al., (2007) found 76% inclusive heritability in the propensity of western bluebirds *Sialia mexicana* to help at some point over the lifespan, while a study of the Tibetan ground tit *Pseudopodoces humilis*, found 47% inclusive heritability in the same trait (Wang & Lu, 2018). Our findings are also towards the low end of estimates of heritability for other behavioural traits, with average h^2 being 23.5% (95% CI: 20.0–27.1) for 476 estimates from 101 publications (Dochtermann et al., 2019). Unlike our study, many previous studies were not able to take non-genetic inheritance routes into account, so some inclusive heritability may be explained by parental

and cultural effects and territory quality (Whiten, 2017; Whiten et al., 2017). Moreover, heritability may have been inflated through previous studies using a single measure of help rather than repeated measures through the lifespan (Åkesson et al., 2008; Engelhardt et al., 2018). The inability to consider non-genetic inheritance routes may contribute to the ‘missing’ heritability in studies of human morphology and disease, whereby genome-wide association studies have consistently failed to find sufficient genetic influence to account for the inclusive heritability of some traits, pointing to alternative routes for heritability (Manolio et al., 2009).

Genuine biological differences between species may also play a role in explaining differences in genetic heritability of helping syndromes. Banded mongooses are obligate cooperative breeders (where pairs never breed independently (Cant et al., 2016)) in contrast to the facultatively cooperative breeders investigated in the wild previously (Charmantier et al., 2007; Sparkman et al., 2012; Wang & Lu, 2018). Fundamental differences between these breeding strategies may lead to differences in the benefits of inhabiting heritable ‘social niches’ (Bergmüller et al., 2010). For example, individuals may adopt a niche to either (1) help in the home territory and potentially inherit the breeding position or (2) disperse early to breed independently. Such niches may be more prominent in facultative than obligate cooperative breeders, as obligate cooperative breeders likely have far fewer opportunities to adopt strategy (2) and breed independently. Concordantly there is no evidence of social niches related to helping and breeding in banded mongooses (Sanderson et al., 2015a). We are not aware of any measures of heritability of cooperation in other obligate cooperative breeders, but future studies will be able to reveal patterns associated with this breeding strategy.

Although genetic heritability explained qualitative contributions to help in male banded mongooses (whether or not individuals helped within a given breeding event), it had little impact on quantitative contributions (the amount of time spent helping within a breeding event) of those that did help. This indicates significant genetic heritability in the propensity to help, while for those that do help, the proportion of time spent helping appears to be determined by immediate environmental and/or internal factors that were not measured in this study. These may include satiety, illness/injury, predation risk and the availability of mating opportunities.

Males show greater heritability and females show stronger effects of the current environment

While male banded mongooses displayed significant genetic heritability in their propensity to help, females did not. This may be because of differences in the costs of helping between the sexes (Hodge, 2007). Specifically, providing pup care leads to reduced body condition,

which appears to have a greater impact on female than male reproductive success (Gilchrist et al., 2004; Hodge, 2007; Hodge et al., 2009; Nichols et al., 2010). Given this stronger link between current conditions and female reproductive success, we should expect females to evolve high plasticity to current conditions, only contributing to care when they can afford to do so energetically, or when their own offspring will likely suffer if they do not provide care (Nichols et al., 2012). Selection may therefore act to shape a behavioural rule, used by all females, that results in them tracking the state of their internal and external environment with their behaviour. Consistent with this prediction, a greater proportion of variance was explained by current environment (represented by communal litter identity) in females than males. A similar pattern occurs in red wolves *Canis lupus rufus* (Sparkman et al., 2012), where males but not females show heritable variation in dispersal probabilities. Red wolf females are smaller than males and hence may be more vulnerable to within-group competition or environmental conditions (Sparkman et al., 2012).

Both environmental and individual factors influenced patterns of helping in males and females. For example, rainfall (which reflects food availability) influenced male propensity to help, males contributed more to babysitting in smaller social groups, and females were more likely to escort if they had given birth to pups in the breeding event. Both sexes were more likely to escort when the litter was larger and hence more escorts were required, and there were quadratic relationships with age in both sexes with young adults contributing most. These effects have been considered extensively in previous studies (Cant, 2003; Gilchrist & Russell, 2007; Hodge, 2007; Nichols et al., 2012) so will not be discussed in detail here, however, they emphasise the flexible nature of helping behaviour, which is often moderated based on immediate conditions (Nichols et al., 2012).

Little evidence for cultural heritability or impacts of permanent environment on helping behaviour

While we found significant genetic heritability for propensity to help, we found very little evidence of cultural heritability of helping behaviour; neither the identity of the escort nor the cultural pedigree explained significant variance in any of our models. Furthermore, whether or not individuals had a stable escort in infancy had no impact on their contributions to cooperation as adults. Together, these results suggest that cooperation is not inherited from escorts through mechanisms such as generalised reciprocity (Rankin & Taborsky, 2009), whereby individuals contribute more to help if they themselves receive more help. A lack of an impact of this ‘secondary inheritance system’ (Whiten, 2017) seems somewhat surprising given the large and durable impact of escorting

on key life history traits and reproductive success in this system (Hodge, 2005; Vitikainen et al., 2019), and with recent work showing that pups inherit their lifelong foraging niche from escorts, not genetic parents (Sheppard et al., 2018). The banded mongoose cultural pedigree is smaller than the genetic pedigree, which could reduce our power to detect cultural inheritance. However, the cultural pedigree is still large, consisting of 672 pup-escort pairs, hence, it seems unlikely that the lack of an effect is because of lack of power. Interestingly, the finding of genetic but not cultural heritability in helping behaviour implies that the ability of individuals to transmit cultural information on foraging niche is to some extent genetically determined.

A lack of an effect of the cultural pedigree on propensity to help does not negate the possibility of cultural inheritance of other aspects of helping behaviour; instead it is possible that the quality or style of care may be culturally inherited. For example, there is abundant evidence from human and non-human primate studies that parenting styles show cultural inheritance based on early-life experiences (Berman, 1990; Fairbanks, 1989; Meaney, 2001). Furthermore, social learning could impact on helping through routes other than the cultural pedigree. For example, individuals may gain information from multiple role models within their social group, rather than just their escort. It is also possible that the propensity to help is influenced by the current social environment, which may contribute to the large effect of the communal litter identity term in our models. Unfortunately, we do not yet have the data required to quantify the potential for social learning outside of escorting relationships.

Our study found no effect of maternal or paternal identity on propensity to cooperate, and little influence of the identity of the social group a potential helper was present in. There is therefore little evidence for an impact of the permanent environment (e.g. territory quality or long-term differences in the social composition of groups) on helping behaviour in banded mongooses. This contrasts with findings from some other species, for example, Kasper et al., (2017a) found that the primary determinants of contributions to help in a laboratory population of cichlids were maternal effects and the permanent environment, with low or negligible impacts of genetic heritability. Similarly, laboratory rats that receive more care as infants become more nurturing as mothers (Champagne & Meaney, 2001). In banded mongooses, maternal effects may be diluted as females give birth in synchrony and appear to suckle and groom pups from the communal litter indiscriminately, hence, pups receive care from individuals other than their mother (Cant et al., 2016). Alternatively, maternal effects may be present but may not be identified by our study. For example, variation between breeding events in maternal stress during pregnancy may upregulate contributions

to helping for one litter but downregulate contributions in another litter from the same mother. However, we currently lack the required data to detect such an effect. Such a situation appears to occur in wild meerkats *Suricata suricatta* where experimentally induced increases in cortisol levels during pregnancy affect the contributions of resultant offspring to alloparental care as adults (Dantzer et al., 2019).

CONCLUSION

The characteristics of our study system allowed us an unusual opportunity to detangle genetic and cultural inheritance, as well as various early life and environmental effects, in a wild population. Despite a seemingly excellent system for transmitting cultural information in the form of one-to-one pup care, we find no evidence for cultural inheritance of individual contributions to helping behaviour, suggesting that mechanisms such as generalised reciprocity do not lead to the heritability of cooperative personalities in this system. Cultural transmission may, however, be important for qualitative aspects of pup care that were not measured here. Genetic heritability in the propensity to help appears to vary substantially between the sexes; males showed low but significant genetic heritability, whilst females showed no detectable genetic heritability. Our results provide new insights into the role of cultural transmission, genetic heritability, early life, environmental and intrinsic effects on the expression of key behaviours in wild populations. Cooperative breeders, particularly those whose life histories allow the separation of genetic and cultural transmission, provide excellent opportunities for future work exploring the relative contributions of different inheritance mechanisms in the development of wild animal behaviours.

ACKNOWLEDGEMENTS

We thank Uganda Wildlife Authority and Uganda Institute for Science and Technology for permission to conduct our research, and the wardens of Queen Elizabeth National Park for continuous support of our long-term study. We thank our field team: F. Mwanguhya, S. Kyabulima, K. Mwesige, R. Businge, S. Ahabyona and the many postgraduate and postdoctoral researchers who have contributed to data collection over the past 21 years.

AUTHOR CONTRIBUTIONS

HJN and JLS conceived the study. MAC managed the field project and JLS, EIV, HM, FJT collected the behavioural data. HJN and DAW collected the genetic data. DAW, KA, JLS and HJN conducted analyses. MAC and HJN obtained funding. HJN wrote the paper with contributions from all authors.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13833>.


DATA AVAILABILITY STATEMENT

Data and R code used in this paper can be found at <https://doi.org/10.6084/m9.figshare.14248784.v1>

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How to cite this article: Nichols, H.J., Arbuckle K., Sanderson J.L., Vitikainen E.I.K., Marshall H.H., Thompson F.J., et al (2021) A double pedigree reveals genetic but not cultural inheritance of cooperative personalities in wild banded mongooses. *Ecology Letters*, 24, 1966–1975. <https://doi.org/10.1111/ele.13833>