

LETTER

Inbreeding depresses altruism in a cooperative society

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Abstract

In some animal species, individuals regularly breed with relatives, including siblings and parents. Given the high fitness costs of inbreeding, evolutionary biologists have found it challenging to understand the persistence of these inbred societies in nature. One appealing but untested explanation is that early life care may create a benign environment that offsets inbreeding depression, allowing inbred societies to evolve. We test this possibility using 21 years of data from a wild cooperatively breeding mammal, the banded mongoose, a species where almost one in ten young result from close inbreeding. We show that care provided by parents and alloparents mitigates inbreeding depression for early survival. However, as adults, inbred individuals provide less care, reducing the amount of help available to the next generation. Our results suggest that inbred cooperative societies are rare in nature partly because the protective care that enables elevated levels of inbreeding can be reduced by inbreeding depression.

Keywords

altruism, inbreeding, cooperation, mating systems, evolution, sociality, alloparenting.

Ecology Letters (2020) **23**: 1460–1467

INTRODUCTION

Habitual inbreeding is rare in the animal kingdom due to the ubiquitous negative impact of inbreeding on fitness, known as inbreeding depression, which results in strong selection for inbreeding avoidance (Pusey & Wolf 1996). However, inbreeding occurs as a regular part of the mating system of a number of species (Avilés & Purcell 2012), raising the question of why such systems evolve. Theory predicts that habitual inbreeding can be favoured when the fitness costs of inbreeding depression are low in comparison to the benefits of inbreeding, which come in the form of higher levels of relatedness between parents and their offspring and allow parents to pass down a greater proportion of their genes (Kokko & Ots 2006; Szulkin et al. 2013). Furthermore, inbreeding also increases local relatedness within animal societies, which can result in inclusive fitness benefits (Kokko & Ots 2006) and favour the spread of altruism (Michod 1980; Wade & Breden 1981; Roze & Rousset 2004). But under what circumstances can inbreeding depression be reduced sufficiently to allow transitions to inbred mating systems?

A key factor that could modulate this transition is the provision of early life care (Avilés & Bukowski 2006). Inbreeding depression is highest under environmental stress (Fox & Reed 2011; Reed et al. 2012), and care may provide a relatively benign environment, mitigating inbreeding depression (Duthie et al. 2016) and leading to a situation whereby inbreeding is favoured. The resultant high levels of inbreeding and relatedness should then favour the evolution of altruism, including the

provision of alloparental care, that could further decrease inbreeding depression in young. This ‘protective altruism’ hypothesis has been proposed to explain the evolution of the inbred cooperative societies observed in social spiders, where dispersal is rare, individuals habitually breed with close relatives and levels of cooperation including alloparental care are extremely high (Avilés & Purcell 2012). It may also play a role in explaining the relatively high levels of inbreeding tolerance found in a handful of cooperatively breeding vertebrates (Nichols 2017). However, so far the possibility that parental care buffers against inbreeding depression has only been tested empirically in a laboratory population of burying beetles *Nicrophorus vespilloides* (Pilakouta et al. 2015), and no studies have focused on investigating interactions between inbreeding and alloparental care. Additionally, both inbreeding depression and the benefits of care are expected to be greater in the wild due to higher levels of environmental stress (Meagher et al. 2000). Consequently, detailed insights into the interplay between inbreeding and care in a wild animal society are needed in order to better understand the conditions under which inbred mating systems might evolve.

A critical assumption of the hypothesis that early life care can lead to the evolution of inbred mating systems (those where frequent inbreeding leads to inbred offspring, parents and alloparents if present) is that care itself does not suffer from inbreeding depression (Pilakouta et al. 2015). Reduced parental care is associated with inbreeding in some species (Margulis 1998; Garcia-Navas et al. 2009; Pooley et al. 2014),

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possibly because inbred individuals have fewer resources available to spend on care. However, the situation may be different in the case of alloparental care. In cooperative breeders, where alloparents contribute substantially to offspring care, there is often intense competition for rare breeding opportunities (Hatchwell & Komdeur 2000). If inbred individuals are less likely to be successful competitors, they may instead direct care towards relatives' offspring in order to maximise their inclusive fitness. Alternatively, inbreeding may retard sexual development, meaning that inbred individuals spend longer as non-breeding helpers. Under such circumstances, high levels of inbreeding could conceivably increase the total amount of care provided to offspring and facilitate evolutionary transitions to inbred cooperative mating systems (Avilés & Bukowski 2006). Such transitions may be particularly likely if care is targeted towards inbred offspring, who will have the lowest fitness in the absence of care (Duthie et al. 2016).

We test the following three predictions resulting from the hypothesis that alloparental care may facilitate the evolution of inbred cooperative societies: (1) care of offspring reduces inbreeding depression; (2) care is directed towards inbred individuals; and (3) care itself is not reduced by inbreeding. To test these predictions, we use an exceptionally large data set (2023 h of observational data coupled with genetic data from 1125 individuals sampled over 21 consecutive years) from a wild population of cooperatively breeding banded mongooses, *Mungos mungo*. This species lives in social groups composed primarily of relatives, with each group containing multiple breeding males and females. Both sexes routinely breed within their natal group, leading to frequent close inbreeding (9% of pups are the product of father–daughter or full-sibling matings (Nichols et al. 2014)). Inbreeding depression occurs for fitness components associated with individual quality (weight and male reproductive success) but not with survival (Wells et al. 2018). One possible explanation for this could be that high levels of early life care may buffer inbreeding depression for survival, which may in turn reduce inbreeding depression to a level whereby the benefits of inbreeding exceed the costs.

Banded mongooses display two distinct forms of offspring care: babysitting and escorting (Cant et al. 2016). For the first 30 days after birth, one or more adults remain at the den as 'babysitters' to protect the communal litter while the rest of the group forages (Fig. 1A). Once pups are mature enough to accompany the group on foraging trips, many form exclusive one-to-one relationships with an adult who feeds, carries,

grooms and protects them from predators (Sheppard et al. 2018). This form of care is unique to this species and is termed 'escorting' (Fig. 1B). Both pups and carers appear to be involved in maintaining escorting relationships, with pups aggressively defending their escorts from others (Gilchrist 2008) and escorts recognising and responding to their pups (Bell 2008; Müller & Manser 2008). The escorting relationship lasts for approximately 2 months. Pups vary in the amount of care they receive from escorts and some pups are not escorted at all (Fig. S1) but instead move between different adults while begging for food. Adults also vary in their contributions to care and some individuals provide no care (Fig. S1). This naturally occurring variation in inbreeding and care makes the banded mongoose an ideal system in which to investigate feedback between alloparental care and inbreeding in the wild.

MATERIALS AND METHODS

Study site and data collection

We use data and samples collected between November 1995 and July 2016 as part of an ongoing study of a wild population of banded mongooses in Queen Elizabeth National Park, Uganda (0°12'S, 27°54'E). The study site comprises approximately 10 km² of scrub on and around the Mweya Peninsula, which contains roughly 200 individual banded mongooses at any one time belonging to 10–12 social groups. At the centre of the study site is a weather station, which collects daily rainfall measurements.

All individuals in the population can be identified on sight due to a unique fur shave or dye pattern (l'Oreal, UK) or colour-coded plastic collar. Markings are maintained by trapping all individuals in the population every 3–6 months (Hodge 2007; Jordan et al. 2010). Body mass (g) is measured without trapping as individuals are habituated to step onto portable scales for a small milk reward. One or two adults in each group are fitted with a 26-g radio collar (<2% of body mass, Sirtrack Ltd.) with a 20-cm whip antenna, which allows groups to be located. Most groups are habituated to human observation within 5m and are visited every 1–3 days to collect detailed individual-based behavioural and life-history data.

Quantifying alloparental care given and received

Reproduction is highly synchronised within social groups, with up to 13 females (median = 3) giving birth together in an



Fig. 1 Banded mongoose caring behaviour. (a) Babysitting, where one or more adults remain at the den to protect all pups in the communal litter; and (b) escorting, where an adult provides one-to-one care for a single pup over a 2-month period. Photograph credits: David Seager and Hazel Nichols.

underground den, often on the same night (Cant *et al.* 2014). This leads to large litters of mixed parentage that are raised by multiple group members including parents and non-parents (Vitikainen *et al.* 2017). Pups do not leave the den during their first month of life, and during this period one or more adult ‘babysitters’ stay with the pups while the rest of the group leaves to forage. Babysitting is important for offspring survival because litters without babysitters are vulnerable to predators or infanticide by rival groups (Marshall *et al.* 2016). Babysitters are identified by either being observed at the den while the rest of the group forages at least 100 m away, or by their absence from the group on foraging trips (Hodge 2007).

When pups are aged between ~30 and ~90 days, they accompany the group on foraging trips and are fed by adult group members. Pups usually form one-to-one relationships with a particular adult, termed an ‘escort’, who feeds, grooms, carries and protects the pup. Escorting is not preferentially directed towards close kin (Vitikainen *et al.* 2017) and individuals that have not reproduced are some of the primary providers of care (Hodge 2007). During the escorting period, groups are visited once or twice per day to record escorting behaviour. Escorting is very conspicuous (Video S1) and is therefore easy to visually identify. Adults are classified as escorting a pup if they spend more than half of a given 20-minute observation period within 0.3m of the focal pup (Vitikainen *et al.* 2017).

Genetic data

The first time individuals are captured, they are fitted with a PIT tag (TAG-P-122IJ, Wyre Micro Design, UK) for permanent identification and their sex is determined through visual inspection. For genetic analysis, a 2-mm tissue sample is taken from the tail tip using surgical scissors and afterwards a dilute solution of potassium permanganate is applied to minimise the risk of infection.

From 1995 to 2016, we collected a total of 1125 tissue samples. These were genotyped for 35–43 microsatellite loci and the resulting data were used to determine parentage as described in Wells *et al.* (2018) and Sanderson *et al.* (2015). Pairwise relatedness values were derived from a maximal nine-generation deep pedigree that included only individuals with all four grandparents known. We then quantified inbreeding directly from the genetic data by calculating standardised multilocus heterozygosity (sMLH) within the R package *inbreedR* (Stoffel *et al.* 2016). sMLH is defined as the total number of heterozygous loci in an individual divided by the sum of average observed heterozygosities in the population for the same loci, with lower values representing less genetically diverse individuals. In our study population, sMLH is strongly correlated with pedigree *f*, and heterozygosity is correlated across loci, indicating that our microsatellites are capturing variation in inbreeding (Wells *et al.* 2018). We used sMLH rather than pedigree *f* as we have previously shown that sMLH tends to outperform pedigree *f* at capturing variance in inbreeding and quantifying inbreeding depression in our mongoose population, partly because the pedigree is much smaller than the number of genotyped individuals (Mitchell *et al.* 2017; Wells *et al.* 2018).

Ethical statement

Our research was carried out under licence 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 Behavioural Research and Teaching and have been approved by the Ethical Review Committee of the University of Exeter. Our trapping procedure has been used over 8,000 times, and tissue samples have been taken from over 1,000 individuals with no adverse effects.

Statistical analysis

We constructed generalised linear mixed models (GLMMs) and generalised additive mixed models (GAMMs) in the R packages *lme4* (Bates *et al.* 2014) and *gamm4* (Wood *et al.* 2017), respectively, to investigate (1) whether care reduces inbreeding depression; (2) whether care is directed towards inbred pups; and (3) whether the provisioning of care is itself impacted by inbreeding. Details of the specific models are provided below. All statistical tests were two-tailed. All of the variables that we analysed are defined in Table S1 and the distributions of key variables across our data set are shown in Figure S1. All of our models were checked for collinearity of predictor variables and validated by inspecting histograms of the residuals and plots of the residuals against predictor variables.

Does care reduce inbreeding depression?

We investigated the impact of escorting care on inbreeding depression for two early life fitness traits: survival to, and weight at, nutritional independence (approximately 90 days of age). Note that we could not investigate a similar impact of babysitting care as it is not possible to determine the survivorship or weight of pups prior to emergence from the den.

The first of these models investigated pup survival to 90 days, which was expressed as a binary response variable. We fitted as predictor variables the amount of escorting care received, pup sMLH and the interaction between escorting and sMLH. Models with and without the interaction term were compared using a likelihood ratio test to determine its significance. Average rainfall over the 30 days prior to birth was also included as a predictor variable because it is strongly associated with pup survival (Wells *et al.* 2018). To account for non-independence among pups, the identity of the pup’s social group and litter was included as random effects. This model incorporated data from 776 pups from 142 litters belonging to 11 social groups.

The second of these models investigated pup body mass at nutritional independence. For logistical reasons, it was not always possible to measure mass at exactly 90 days, so we used the closest available measurement (see Table S1 for details). To account for growth over this period, age at weighing (in days) was included in the model as a covariate. As above, the amount of escorting care received, pup sMLH and the interaction between escorting and sMLH were included as predictor variables. We then tested whether care reduced

inbreeding depression for body mass by comparing models with and without an interaction between care and sMLH using a likelihood ratio test. Average rainfall over the first 2 months of an individual's life was also included as a predictor variable due to the importance of early-life rainfall on growth (Gilchrist 2004). To enable this model to converge, both rainfall and age at weighing were standardised by subtracting the mean and dividing by the standard deviation (Harrison et al. 2017). To account for non-independence among pups, both social group and litter were included as random effects. We modelled pup weight with a negative binomial error distribution to account for heterogeneity in residuals. This model incorporated data from 443 pups from 120 litters belonging to 10 social groups.

Do inbred pups receive more care?

We tested whether escorting care is preferentially directed towards inbred pups. This analysis focused on escorting because this behaviour is directed towards specific individuals, whereas babysitting is directed towards an entire litter of pups which are not all equally inbred. The amount of escorting care received was fitted as a response variable in a binomial GLMM. Predictor variables were sMLH, sex, litter size, and the average rainfall over the 60-day escorting period and the 14 days before it (Vitikainen et al. 2017). Rainfall was standardised by subtracting the mean and dividing by the standard deviation. As in previous models, group and litter were included as random effects. The model incorporated data from 762 pups from 138 litters belonging to 11 social groups.

Is the amount of care provided by adults affected by inbreeding?

We tested whether inbreeding influences the extent to which potential carers provide alloparental care in the forms of babysitting and escorting. These analyses were implemented using GAMMs. Individuals were identified as potential carers if they were at least 6 months old at the start of the care period and were in the same social group as the litter. Contributions to babysitting and escorting showed zero inflation (Figure S1). To account for this, we constructed two models for each type of care; (1) A binary model analysed whether individuals were observed to provide care to a litter on at least one occasion (1 = care provided, 0 = no care provided); (2) For those individuals that were observed to provide care, their contributions to care were fitted as a response term in a binomial model using the *cbind* function in R (observed caring x times and not caring $n-x$ times, where n is the number of observations). We ran two models rather than using a single binomial model accounting for zero inflation because the latter cannot incorporate non-monotonic response variables (see below).

We fitted sMLH as an explanatory variable, together with other variables that have been shown to affect the provision of care in previous studies (age, parentage, rainfall, relatedness and litter size, see Table S1 for definitions; Nichols et al. 2012; Vitikainen et al. 2017). The relationship between age and care is non-monotonic, increasing sharply in early life before levelling off or decreasing. To account for this, we modelled age using a thin-plate regression spline. Rainfall

(mm) was taken as the average over the 30- or 60-day care period and the 14 days prior to it for babysitting and escorting, respectively, and in both cases it was standardised by subtracting the mean and dividing by the standard deviation. Litter size was used in the models of escorting but not of babysitting because it is not possible to count the number of pups in the litter before they emerge from the den. To account for non-independence, the identity of the social group, litter and individual was fitted as random effects. We constructed separate models for males and females because the extent to which the two sexes provide care is strongly influenced by their differing life histories (Hodge 2007). Furthermore, rainfall influences the caring behaviour of female breeders and non-breeders differently (Nichols et al. 2012). We therefore fitted an additional interaction between rainfall and parentage.

The binary model of male babysitting was based on 4006 samples, where each sample represents all care provided to a specific litter by a given individual. Of these, 2270 included some babysitting and so were included in the binomial model. The male data set included 395 potential babysitters of 389 litters in 14 social groups. The binary model of female babysitting was based on 2486 samples, of which 1,198 included some care so were included in the binomial model. The female data set included 292 potential babysitters over 377 litters belonging to 14 social groups.

The binary model of male escorting was based on 1804 samples, of which 540 included some care and so were also included in the binomial model. The male data set included 310 potential escorts of 156 litters in nine social groups. The female models were based on 1206 samples of which 244 included some care so were included in the binomial model. The female data set included 233 potential escorts over 156 litters belonging to 10 social groups.

RESULTS

Does care reduce inbreeding depression?

We find that care provided by escorts significantly reduces the impact of inbreeding depression on pup survival (sMLH:care $\beta = -4.23$, log likelihood ratio (2LL1) = 6.29, $P = 0.012$, Fig. 2 and Table S2) and tends towards reducing a negative impact of inbreeding on pup weight (sMLH:care $\beta = -0.27$, 2LL1 = 2.90, $P = 0.088$, Fig. S2 and Table S3). Without care from a stable escort, only around a quarter of inbred offspring survive to independence, whereas with average levels of escorting, inbred pups have similar survival chances to outbred pups, with around three quarters surviving. By contrast, escorting has little impact on the survival of outbred pups. Thus, early life care restores the survival of inbred pups to levels seen in outbred pups, mitigating inbreeding depression in a wild population and allowing more pups to reach adulthood.

Do inbred pups receive more care?

If counteracting inbreeding depression is an evolved benefit of care, we would expect alloparental care to be directed

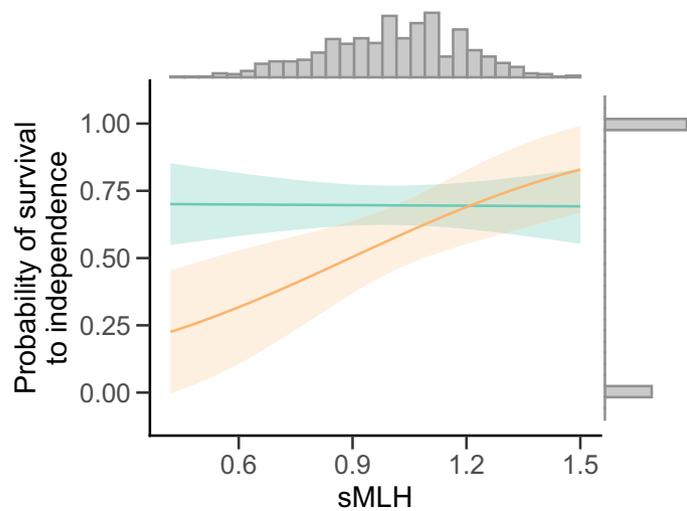


Fig. 2 Care provided by escorts mitigates inbreeding depression for early survival. Shown is the probability of pup survival to 90 days for offspring receiving no escorting care (in orange) versus offspring receiving the average non-zero amount of escorting care, that is, they were escorted during 62% of observations (in green). To quantify inbreeding, we use standardised multilocus heterozygosity (sMLH) measured at 35–43 microsatellite loci, whereby inbred individuals have low sMLH values. Trend lines show predicted values from the fitted model, and the shaded regions show 95% CIs. Grey marginal histograms show the distribution of data.

disproportionately towards inbred pups, as these individuals will benefit the most from receiving care. However, we find no evidence that inbred pups receive more alloparental care than outbred pups (sMLH $\beta = 0.15$, $2LL_1 = 0.04$, $P = 0.84$, Table S4).

Is the amount of care provided by adults affected by inbreeding?

Finally, we show that inbreeding is associated with reductions in both babysitting and escorting. Specifically, relatively inbred individuals of both sexes are less likely to babysit (males: sMLH $\beta = 0.97$, $2LL_1 = 8.86$, $P = 0.003$; females: sMLH $\beta = 0.69$, $2LL_1 = 4.73$, $P = 0.030$, Fig. 3A, Table S5A and B) and inbred males are also less likely to escort a pup (sMLH $\beta = 1.36$, $2LL_1 = 5.23$, $P = 0.022$, Fig. 3B, Table S6A), while the likelihood of escorting increases marginally with inbreeding in females (sMLH $\beta = -1.20$, $2LL_1 = 4.37$, $P = 0.037$, Fig. 3B, Table S6B). For those individuals that do provide care, inbred males provide less babysitting (sMLH $\beta = 0.42$, $2LL_1 = 5.62$, $P = 0.018$, Table S5C), while inbreeding is not associated with the amount of babysitting provided by females (sMLH $\beta = -0.12$, $2LL_1 = 1.04$, $P = 0.308$, Table S5D) nor the amount of escorting provided by either sex (males: sMLH $\beta = 0.30$, $2LL_1 = 0.53$, $P = 0.47$; females: sMLH $\beta = -0.17$, $2LL_1 = 0.10$, $P = 0.76$, Table S6C and D). As more than two thirds of all care are provided by males, the overall effect of inbreeding is therefore to reduce the total amount of care provided to offspring.

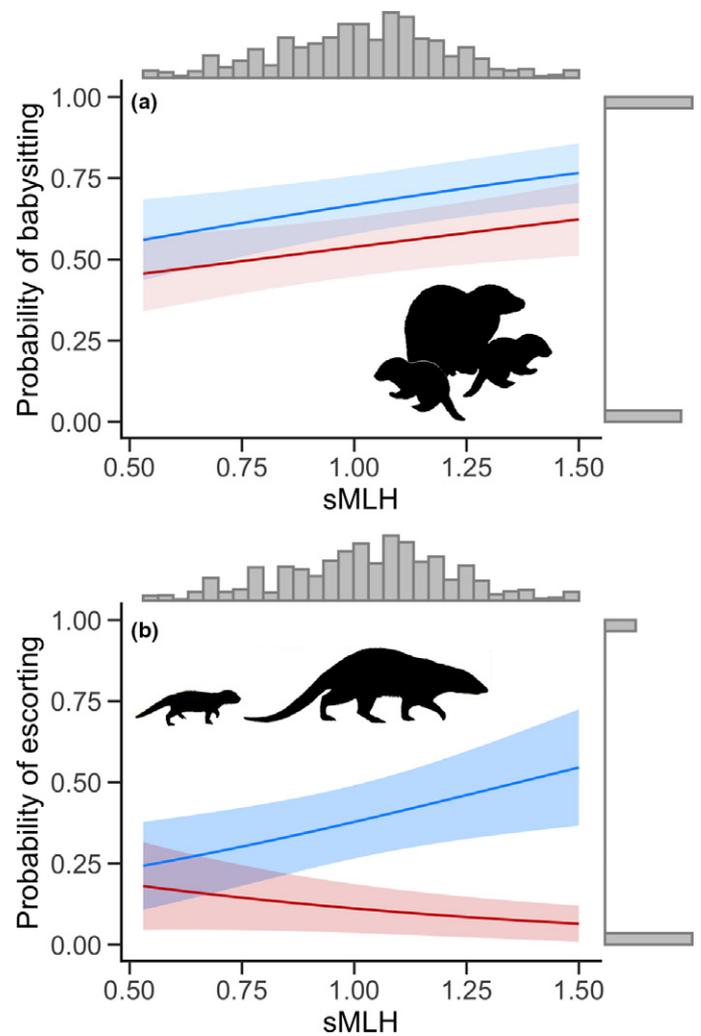


Fig. 3 Inbreeding reduces the provision of alloparental care. Shown is the probability of providing (a) babysitting care and (b) escorting care, conditional on standardised multilocus heterozygosity (sMLH) and plotted separately for males (in blue) and females (in red). Trend lines show predicted values from the fitted models and the shaded regions refer to the associated 95% CIs. Grey marginal histograms show the distribution of data. Inbred individuals (low sMLH) of both sexes were less likely to be observed babysitting, whereas escorting was negatively associated with escorting in males but marginally positively associated with escorting in females.

Could our results be confounded by covariance between inbreeding and the number of observations of a given individual?

It is conceivable that a relationship between inbreeding and care received or provided could result as an artefact of covariance between inbreeding level and the number of times an individual was observed during the period of care. Such a relationship could arise, for example, if inbred individuals are more likely to die during the caring period. To test for this, we constructed three separate zero-truncated Poisson GLMMs in which the respective response variables were (1) the number of times a pup was observed, (2) the number of times a potential babysitter was observed; and (3) the number of times a potential escort was observed. sMLH was included as the sole

predictor variable together with individual, litter and social group as random effects. We found that sMLH was not significantly associated with any of the three variables (*number of times a pup was observed*: sMLH $\beta = 0.53$, $P = 0.51$; *number of times a potential babysitter was observed*: males sMLH $\beta = 0.001$, $P = 0.96$, females sMLH $\beta = 0.004$, $P = 0.89$; *number of times a potential escort was observed*: males sMLH $\beta < 0.001$, $P = 0.99$, females sMLH $\beta > -0.001$, $P = 0.99$). This suggests that our results are not confounded by covariance between the number of times a focal individual is observed and the level of inbreeding of that individual.

DISCUSSION

We find that early life care mitigates inbreeding depression in banded mongooses, with care provided by escorts boosting the survival prospects of inbred pups to levels seen in outbred pups. This effect is likely to result from one-to-one care creating a relatively benign environment; pups are fed and protected by their escorts who provide vigilance and carry pups to protect them from predators (video S1). By contrast, pups without an escort beg for food from multiple adults in the group and are rarely carried so are likely to be more vulnerable to both malnutrition and predation. Similar results have been found in laboratory populations of burying beetles, where maternal care disproportionately increases the survival (Pilakouta et al. 2015) and weight (Mattey et al. 2018) of inbred offspring. Compensatory care therefore appears to allow parents and alloparents to counteract the negative effects of poor offspring genetic quality (Mattey et al. 2018). This in turn may reduce the strength of selection against inbreeding avoidance, potentially tipping the balance in favour of evolving inbred cooperative societies such as those seen in social spiders (Avilés & Purcell 2012).

Care buffering the effects of inbreeding depression may in part explain why we find relatively high levels of inbreeding in banded mongooses, where 66% of individuals have non-zero inbreeding coefficients (Wells et al. 2018). However, care is unable to completely mitigate inbreeding depression, as inbred yearlings are lighter and inbred males have lower reproductive success (Wells et al. 2018), which may explain why outbreeding appears to be preferred (Nichols et al. 2014; Sanderson et al. 2015). There is little work on the influence of alloparents in other cooperative breeders, but in meerkats, *Suricata suricatta*, the presence of allolactators influences the growth of inbred and outbred pups differently, although the relationship is not clear-cut and carers do not appear to mitigate the negative effects of inbreeding (Nielsen et al. 2012). However, Nielsen et al. (2012) investigated a single form of alloparenting in a species with complex cooperative care and it is possible that other forms of care, such as pup feeding, at least partially compensate for inbreeding depression. Alternatively, cooperative care may fail to buffer inbreeding depression in meerkats, explaining why individuals do not breed with related group mates; instead, inbreeding primarily occurs between unfamiliar lesser relatives after dispersal to new groups (Nielsen et al. 2012). Future studies investigating behavioural interactions between carers and offspring in a range of species will reveal the potential for alloparenting to buffer inbreeding depression on a wider scale.

In banded mongooses, we find that care is not preferentially directed towards inbred pups. One possible explanation for this could be that carers are unable to discriminate inbred from outbred offspring. This is in contrast to burying beetles, where begging is impacted by inbreeding, and (outbred) mothers provide more care to inbred broods (Mattey et al. 2018). In burying beetles, entire broods are either inbred or outbred, so mothers may adjust care to the need of the brood as a whole by assessing overall begging rates, rather than being able to identify inbred individuals from within the brood. In banded mongooses, communal litters are of mixed parentage, so inbreeding levels vary among littermates and inbred pups may be difficult to identify. Interestingly, inbred pups are no less likely to receive help than outbred pups, which might be expected if poor quality pups are outcompeted for access to carers (Gilchrist 2008). This may be because escorting is a two-way interaction, with considerable input from carers in establishing and maintaining bonds (Müller & Manser 2008). Understanding how genetic traits are communicated in this species and exploring the potentially complex interactions between pups and their escorts represent promising avenues for future research.

A key assumption of the hypothesis that early life care may facilitate transitions to inbred mating systems is that care itself is not reduced by inbreeding depression. However, we find that inbred adults provide less care to pups. Low levels of escort care increase pup mortality (Gilchrist 2004; Hodge 2005) and litters repeatedly left without a babysitter never survive (Marshall et al. 2016). A lack of care therefore reduces pup fitness and also impacts on breeders and alloparents, who lose direct and indirect fitness respectively. Our results therefore suggest that inbreeding depression can affect all individuals in a social group via its influence on alloparental care. Similar effects of inbreeding on parental care have been reported in laboratory populations of burying beetles (Mattey et al. 2018) and oldfield mice *Peromyscus polionotus* (Margulis 1998). There is also mounting evidence for indirect genetic effects, whereby genes expressed in one individual impact on the expression of a trait in others, with individuals suffering fitness costs as a result of interacting with inbred individuals even when they themselves are outbred (Mattey et al. 2013; Richardson & Smiseth 2017; Mattey et al. 2018). Such effects are likely to be particularly complex and far-reaching in group-living species where individuals interact with many different partners with whom they may cooperate or compete at different time points in their lives.

While the relative costs of inbreeding may be elevated due to the negative effect of inbreeding on alloparental care, this is unlikely to be the only factor governing the evolution of inbreeding avoidance and tolerance. For example, simulations suggest that inbreeding avoidance behaviours are less likely to evolve where they entail a high cost (Duthie & Reid 2016). In naked mole-rats *Heterocephalus glaber* and social spiders, the relative costs of dispersal to form new outbred groups are high due to vulnerability to predation and landscape barriers (Avilés & Purcell 2012; Ingram et al. 2015), which likely contribute to the relatively high levels of inbreeding seen in these species. In banded mongooses, individuals that disperse to form new groups have almost triple the mortality rates of

those that remain in their natal group (Cant *et al.* 2013). Similarly, while inbreeding can be avoided by mating outside of the social group, such matings tend to occur during violent intergroup encounters and so carry a risk of injury (Nichols *et al.* 2015; Thompson *et al.* 2017). In banded mongooses, relatively high inbreeding rates may have therefore evolved due to the high costs of inbreeding avoidance, in addition to a buffering effect of care on inbreeding depression.

To conclude, theory predicts that inbreeding should favour the evolution of altruistic behaviours as long as the benefits of altruism afforded by kin selection are sufficient to mitigate inbreeding depression (Wade & Breden 1981; Roze & Rousset 2004; Kokko & Ots 2006). We show that this expectation is partly fulfilled, in that alloparental care increases the survivorship of inbred pups. However, the benefits of this system are curtailed in an unexpected way, with inbred individuals showing reduced caring behaviour. The causal relationship between inbreeding and sociality might therefore go both ways: helping may affect the severity of inbreeding depression in offspring and inbreeding may affect the amount of care provided by helpers. Thus, inbreeding depression is not only limited to inbred individuals but also impacts offspring produced during that individual's lifetime, regardless of how inbred those offspring are. Such cross-generational effects may serve to magnify inbreeding depression and could help to explain why inbreeding is rare among species with alloparental care, despite theoretical predictions to the contrary.

ACKNOWLEDGEMENTS

We are grateful to Uganda Wildlife Authority and Uganda National Council for Science and Technology for granting permission to carry out our research and to the Wardens of Queen Elizabeth National Park for providing logistical support.

AUTHORSHIP

H.J.N., D.A.W. and J.I.H. conceptualised the study and wrote the original draft; D.A.W. conducted formal analysis and visualisation; M.A.C., J.I.H. and H.J.N. provided resources, acquired funding and administered the project; H.J.N., D.A.W., M.A.C. and J.I.H. reviewed and edited the manuscript; J.I.H. and H.J.N. supervised the study.

FUNDING INFORMATION

This work was supported by a Deutsche Forschungsgemeinschaft (DFG) standard grant (HO 5122/5-1), a Natural Environment Research Council (NERC) Standard Grant (NE/J010278/1), a dual PhD studentship from Liverpool John Moores University, a Leverhulme International Fellowship (IAF-2018-006) and a Humboldt Research Fellowship for Experienced Researchers awarded by the Alexander von Humboldt Foundation.

CONFLICT OF INTERESTS

The authors declare no competing interests.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/ele.13578>.

DATA AVAILABILITY STATEMENT

Data and R code used in this paper can be found at the Figshare Repository: <https://doi.org/10.6084/m9.figshare.12562820>.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Editor, Minus van Baalen

Manuscript received 12 February 2020

First decision made 7 May 2020

Manuscript accepted 17 June 2020