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Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose

Sarah J. Hodge*

Large Animal Research Group, Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

Helpers in cooperative and communal breeding species are thought to accrue fitness benefits through improving the condition and survival of the offspring that they care for, yet few studies have shown conclusively that helpers benefit the offspring they rear. Using a novel approach to control for potentially confounding group-specific variables, I compare banded mongoose (*Mungos mungo*) offspring within the same litter that differ in the amount of time they spend with a helper, and hence the amount of care they receive. I show that pups that spend more time in close proximity to a helper are fed more, grow faster and have a higher probability of survival to independence than their littermates. Moreover, high growth rates during development reduce the age at which females breed for the first time, suggesting that helpers can improve the future fecundity of the offspring for which they care. These results provide strong evidence that it is the amount of investment *per se* that benefits offspring, rather than some correlate such as territory quality, and validate the assumption that helpers improve the reproductive success of breeders, and hence may gain fitness benefits from their actions. Furthermore, the finding that helpers may benefit offspring in the long-term suggests that current studies underestimate the fitness benefits that helpers gain from rearing the offspring of others.

Keywords: cooperative breeding; helping; banded mongoose; *Mungos mungo*; fitness benefits

1. INTRODUCTION

In cooperative and communally breeding species, group members, known as helpers, assist in rearing offspring that are not their own (Brown 1987; Koenig & Dickinson 2004). This unusual breeding system is thought to evolve because helpers accrue direct and/or indirect fitness benefits through improving the reproductive success of breeders; either by improving the condition and survival of the offspring for which they care, or by increasing the rate at which offspring are produced (Brown 1987; Emlen 1991). Consequently, it is central to our understanding of the evolution of cooperative breeding that helpers enhance reproductive success, yet relatively few studies have provided conclusive evidence that the actions of helpers convey tangible benefits to recipients (Magrath & Yezerinac 1997; Cockburn 1998).

Measuring the effect of helpers on reproductive success is surprisingly difficult. Early attempts investigated the relationship between helper number and the number of offspring produced by breeders (Brown 1987; Emlen 1991). However, such simple correlations do not control for group-specific variables, such as territory quality and breeder experience, which may also influence offspring production (Brown 1987; Cockburn 1998). Furthermore, helpers have been shown to vary widely in the amount of care that they provide (Heinsohn & Legge 1999; Cant & Field 2001), but correlating helper number with offspring production does not allow for variation in helping effort (Magrath & Yezerinac 1997; Cockburn 1998). The limitations of correlational studies were highlighted in a study of rufous vangas (*Schetba rufa*), where a positive relationship between helper number and offspring production disappeared after controlling for variation in territory quality, breeder experience and helper effort (Eguchi *et al.* 2002).

Multivariate analyses and experimental manipulations have been used in a number of studies to control for potential confounding variables. Although some have produced good evidence that helper number has a positive influence on reproductive success (Emlen & Wrege 1991; Mumme 1992; Komdeur 1994; Clutton-Brock *et al.* 2001), no relationship was found in others (Leonard *et al.* 1989; Walters 1990; Legge 2000). Moreover, experimental and statistical approaches have their limitations, since it is often impossible to determine whether it is the help provided, or the simple presence of helpers, that enhances offspring production (Mumme 1992). Other studies have utilized variability in helper contributions and compared equally sized groups that differ in the amount of care that subordinates provide. Results so far have been mixed. In some, offspring production was found to be higher in groups with good helpers (Komdeur 1994; Innes & Johnston 1996), but in others increased helper contributions failed to enhance the number of offspring produced (Magrath & Yezerinac 1997).

A potentially powerful way of teasing apart the effect of helpers from other confounding variables is to compare the growth and survival of offspring that receive different amounts of care. If the care that offspring receive differs within the same litter or brood, it may be possible to investigate how the type and amount of help provided affects the success of offspring, while keeping potentially

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* (sjh94@cam.ac.uk).

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confounding group-specific variables constant. Comparing offspring in this way allows the causal mechanisms behind any fitness benefits to be identified, which is necessary to confirm that it is the amount of help received rather than simply the presence of helpers that improves offspring fitness (Innes & Johnston 1996). Unfortunately, as littermates generally receive similar amounts of help in cooperatively breeding species, such comparisons are rarely possible in wild populations.

In this paper, I describe the effect of helpers on offspring success in the banded mongoose (*Mungos mungo*), a small (<2 kg), diurnal, communally breeding mongoose that lives in groups of 8–28 individuals (Cant 2000). The banded mongoose provides a rare opportunity to investigate whether helpers benefit offspring because, unlike most cooperative breeders, care is unequally distributed among offspring within the same litter. All banded mongoose pups are initially reliant on older group members for food and protection. However, while some pups form conspicuous associations with helpers (termed 'escorts'), that on a given day provide care almost exclusively to one particular pup (Gilchrist 2004), others rarely have an escort and spend a large proportion of the pup care period moving between group members begging for food items. Previous work on this species suggests that pup survival is positively correlated with the number of days spent with an escort (Gilchrist 2004), but as this analysis did not compare within litters, it suffers from the same potential problems as the studies outlined above. Here, I utilize the natural variation in the time that banded mongoose offspring spend with an escort to investigate whether helpers benefit offspring. Specifically I ask whether pups that spend a large proportion of the pup care period with an escort: (i) receive more food; (ii) grow faster; (iii) survive better and (iv) reproduce earlier than their littermates.

2. MATERIAL AND METHODS

This study was conducted on a wild population of 421 individually marked banded mongooses living in eight social groups in the Queen Elizabeth National Park, Uganda (0 12′S; 27 54′E). Banded mongooses breed throughout the year, and in a given breeding attempt up to ten adult females per group give birth in the same den, usually on the same day (Cant 2000). The communal litter of up to 16 pups (mean ± s.e. $=8.4\pm0.75$, $n=37$ litters) are, therefore, of mixed parentage, but are all exactly the same age. Until they are three months old pups are cared for by older group members, who provision them with prey items and protect them by attacking and chasing approaching predators and carrying them away from danger. The majority of care is provided by non-breeding yearling males (Gilchrist 2001, Hodge 2003), although some care is provided by males and females who bred in the current breeding attempt. There is no evidence to suggest that potential parents preferentially care for their own offspring (Gilchrist 2004) and, as such, all individuals who provide care can be considered 'helpers', regardless of whether they bred in the current breeding attempt (following Jennions & Macdonald 1994; Cockburn 1998; Russell 2004). Helpers invariably provide care to the closest pup (Gilchrist 2004), so those pups that spend more time in close proximity to a helper will receive more care. All study animals were habituated to close observation, and between February 2000 and March 2002, I collected data on the growth and survival of 71 pups from 11 breeding attempts.

(a) *Data collection*

(i) *Determination of pup escort status*

Data were collected during the 'feeding period', which began when pups first foraged with the group (at approximately four weeks of age) and ended when pups could forage independently at 12 weeks. Pups were observed throughout the morning foraging session (for 3–4 h); during this period, the identity and distance to the nearest adult neighbour was recorded for each foraging pup every 5 min. At the end of each observation session, pups that were within 30 cm of the same individual for more than 50% of scans were classed as having an escort for that day, and the remainder were classed as having no escort for that day. As pups actively follow adults that provide them with care (Gilchrist 2004), pups were only classified as having an escort if they spent more than 50% of the session close to the *same individual*. This excluded pups that were simply standing close to an adult at a given point in time, but were not receiving care. At the end of each breeding attempt, I calculated the proportion of observation days that each pup had an escort (the 'escort index'), which was a continuous variable, ranging from 0 to 1. Although some pups spent the entire two month feeding period with the same helper, and others switched between different helpers, I use the number of days that a pup had an escort as a proxy of care, regardless of whether the identity of the helper changed across days.

(ii) *Pup feeding*

During the feeding period, continuous 20 min focal watches were conducted on pups, to record the number and size of prey items which they were fed. Banded mongooses are primarily insectivorous and the majority of food items fed to pups are beetles and millipedes (Rood 1975). Food items were divided into three size categories: small (items fitting entirely within the mouth of an adult), medium (less than 50% of the prey item visible outside the adult's mouth) and large (more than 50% of the prey item visible outside the adult's mouth). The mean wet mass of each size category was calculated from the measurements of 154 prey items (small 0.23 g; medium 0.85 g; large 5.10 g), and this was used to estimate the biomass of prey items fed. A minimum of six focal watches were conducted on each pup during the feeding period.

(iii) *Collection of weight data*

Pups were habituated to step onto a portable weighing balance allowing their weight to be obtained before the group foraged in the morning, and again at the end of the morning, providing a measure of weight gain over the foraging session.

(b) *Statistical analyses*

To investigate whether the presence of an escort improved the food intake, growth and survival of pups, I compared pups within the same litter that differed in the proportion of days that they were escorted. Pups with an escort index above the median (0.6) were classified as having a 'high' escort index and the remainder were classified as having a 'low' escort index. The average values for pups with a high and low escort index were then compared within litters, which allowed group-specific factors such as territory quality, group size and environmental conditions to be controlled. However, within litter comparisons do not control for initial variation in offspring quality, which may influence both the probability that a pup gets an escort and their subsequent growth and survival. To control for this I conducted two further analyses. First, I compared the same pup on mornings when it had an escort with mornings when it did not. Second, I controlled for any effect of differences in pup quality by including pup weight prior to the onset of the feeding period (at first emergence from the natal den), and escort index sequentially in multivariate models. Multivariate analyses were performed in GENSTAT 5.4.2 (GENSTAT 1993). Group and litter identity were specified as random terms in mixed models. Normally distributed data were analysed using linear mixed models (LMM) with an identity link function, and binomial data were analysed using generalized linear mixed models (GLMM) with a logit link function. In all mixed models, variance components were estimated using the restricted maximum likelihood (REML) method.

For all multivariate analyses, the escort index of each pup was fitted as a continuous variable. The following potential explanatory terms were also fitted, although not all terms were included in every model: litter size at emergence; pup weight at emergence (controlled for age at emergence); helper number (total group members older than six months); total rainfall during the feeding period (mm); mean biomass of prey items fed per hour during the feeding period ($g\,h^{-1}$) and pup sex. All potential explanatory terms were entered into the model and dropped sequentially until only those terms that explained significant variation remained. All two-way interactions were tested, but are only included in tables if found to explain significant variation. Effect sizes are given for significant terms, and, for normally distributed data, should be interpreted as the change in unit y for a unit change in x. For analysis of pup survival, effect sizes refer to the change in the logit of y for a unit change in x. Means are quoted ±1 s.e. unless otherwise stated. The following multivariate analyses were conducted:

Pup feeding: To test whether pups with a higher escort index were fed at a higher rate, I calculated the mean biomass of prey items fed per hour to each pup during the peak pup feeding period (between 35 and 50 days). Pup age has no significant influence on the rate at which they are fed during the peak feeding period (linear regression: $F_{1,174}=0.07$, $p=0.79$). The mean biomass of prey items fed per hour was transformed with natural logarithms to ensure normality, and fitted as the response term in a LMM.

Pup growth: To obtain growth rates ($g\,d^{-1}$) for each pup between emergence and independence, I took the gradient of the linear regression between pup age and weight (the relationship between age and weight is linear until pups are six months old). Growth rates were only calculated if the pup was weighed four or more times during the feeding period (mean = 16.2 weights per pup, range 4–37). To test whether pups that spent a high proportion of time with an escort had a higher growth rate, I fitted growth rate as the response term in a LMM. I also investigated whether escort index had a positive influence on pup weight at independence, by fitting the mean weight of pups between 90 and 97 days of age as the response term in LMM.

Pup survival: To investigate whether a high escort index increased the probability that a pup survived to independence, I fitted pup survival (1 = survived, 0 = died) as the binomial response in a GLMM, with 1 as the binomial denominator.

Future reproduction: As the sample of pups that survived to 18 months for whom escort data were available was too low for statistical analysis it was not possible to look at the influence of the time spent with an escort on future reproduction directly. However, I investigated this indirectly, by asking whether female weight at independence influenced their age of first conception. Using data from 17 females born early in the study, I fitted whether each female conceived before 18 months of age (1 = yes; 0 = no) as the binomial response in a generalized linear model with 1 as the denominator. The weight of the female at independence and emergence were fitted as potential explanatory terms.

3. RESULTS

(a) *Pup feeding*

The amount of food that pups received from helpers throughout the feeding period was highly variable, ranging from 0 to $16.77\,g\,h^{-1}$ (mean ± s.d. = $3.75\pm3.73\,g\,h^{-1}$; $n=62$ pups). Pups with a high escort index were fed a significantly higher mean biomass of food items per hour than pups with a low escort index when compared within litters (high = $2.44\pm0.49\,g\,h^{-1}$; low = $1.79\pm0.49\,g\,h^{-1}$; paired t-test: $t=2.55$, $n=9$ litters, $p=0.034$). The positive effect of escorts on pup feeding was significant when escort index was included as a continuous variable in a LMM, but none of the other terms included in the model had a significant influence on the rate at which pups were fed. Pups also received a greater biomass of prey items on days when they had an escort, compared to days when they had no escort (escort day = $0.84\pm0.23\,g\,h^{-1}$; non-escort day = $0.25\pm0.07\,g\,h^{-1}$; Wilcoxon signed ranks test: $W=231.5$, $n=24$, $p=0.005$).

(b) *Pup growth*

Between emergence and independence, pups gained an average of $4.0\pm0.2\,g\,d^{-1}$ (range -0.4 to $7.9\,g\,d^{-1}$; $n=63$ pups). Within litters, pups with a high escort index had significantly higher mean growth rates than those with a low escort index (high = $4.27\pm0.49\,g\,d^{-1}$; low = $2.82\pm0.61\,g\,d^{-1}$; paired t-test: $t=2.52$, $n=9$ litters, $p=0.04$), and escort index had a significant positive influence on pup growth, even when the positive effect of weight at emergence was controlled for in a LMM (table 1). Pups with a high escort index were also significantly heavier at independence than those with a low escort index when compared within-litters (high = 510.8 ± 23.8 g; low = 448.1 ± 38.7 g; paired t-test: $t=3.36$, $n=7$ litters, $p=0.015$) and this result held when escort index was included as a covariate in a LMM (table 1). Furthermore, on average, pups gained a greater percentage of their body weight per hour on days when they had an escort, compared to days when they had no escort (escort day = $4.67\pm0.58\%$; non-escort day = $3.33\pm0.47\%$; paired t-test: $n=22$, $t=2.31$, $p=0.031$), but did not differ in weight at the beginning of the foraging session (escort day = 225.6 ± 11.3 g; non-escort day = 224.7 ± 14.4 g; paired t-test: $t=0.12$, $n=22$, $p=0.90$).

(c) *Pup survival*

Pup survival was low: of 242 pups that emerged during the course of this study, only 43% survived to independence.

Table 1. Factors affecting A, the biomass of food items fed to pups throughout the feeding period; B, pup growth and C, pup weight at independence.

(Effects are only given for significant terms in the minimal model. A, biomass fed—analysis was conducted on the mean feeding rates of 54 pups over 10 breeding attempts; B, pup growth—analysis was conducted on the growth rates of 63 pups from nine breeding attempts and C, pup weight at independence—analysis was conducted on the mean independence weight of 30 pups from nine breeding attempts.)

	A: biomass fed (g h^{-1})		B: growth (g d^{-1})		C: weight at independence (g)	
explanatory terms	Wald statistic (χ^2) (d.f.$=$1,53)	p	Wald statistic (χ^2) (d.f.$=$1,62)	p	Wald statistic (χ^2) (d.f.$=$1,29)	p
escort index	4.27	0.039	4.50	0.034	12.46	<0.001
helper number	2.94	0.09	1.76	0.19	0.16	0.69
weight at emergence (g)	1.31	0.25	5.47	0.019	3.18	0.08
pup sex (male : female)	0.02	0.89	0.05	0.81	1.08	0.30
litter size at emergence	3.30	0.07	0.23	0.63	0.07	0.79
rainfall during feeding period (mm)	0.07	0.79	0.43	0.51	0.15	0.70
mean biomass fed (g h^{-1})	N/A	N/A	0.81	0.37	0.06	0.80
minimal model	effect size	s.e.	effect size	s.e.	effect size	s.e.
constant	0.18	0.070	3.88	0.39	485.40	20.54
escort index	0.40	0.19	1.11	0.52	159.2	45.09
weight at emergence	—	—	0.018	0.0077	—	—

Of 23 pups for whom the cause of death was known, predation by marabou storks (*Leptoptilus crumeniferus*) and monitor lizards (*Varanus niloticus*) was observed directly on 19 occasions, and on four occasions pups became separated from the group and were assumed to have been subsequently depredated. During this study, only two pups lost weight prior to disappearance and were thought to have died of starvation.

Pups with a high escort index had a significantly higher probability of survival to independence than their littermates with a low escort index (high$=0.80\pm0.10$; low$=0.45\pm0.14$; paired t-test: $t=2.32$, $n=9$ litters, $p=0.049$). Multivariate analyses confirmed that escorts have a positive effect on pup survival (table 2), and showed that the probability of survival to independence increased by 4.5% for each 10% increase in the number of days spent with an escort.

Table 2. Factors affecting the probability of pup survival to independence.

(Effects are only given for significant terms in the minimal model. Analysis was conducted on the survival of 72 pups from 12 breeding attempts.)

explanatory terms	Wald statistic (χ^2)	d.f.	p
escort index	4.60	1,71	0.032
weight at emergence (g)	0.94	1,71	0.33
pup sex (male : female)	0.82	1,71	0.36
mean biomass fed (g h^{-1})	0.81	1,71	0.37
rainfall during feeding period (mm)	0.72	1,62	0.40
litter size at emergence	0.21	1,71	0.65
helper number	0.05	1,71	0.83
minimal model	effect size	s.e.	
constant	0.58	0.36	
escort index	1.58	0.73	

(d) *Future reproduction*

Female pups had a significantly higher probability of conceiving before 18 months of age if they were relatively heavy at independence (GLM: $F_{1,22}=9.56$, $p=0.002$, $R^2=22.7$). A 50 g increase in weight at independence resulted in a 14.5% increase in the probability that a female would conceive, but weight at emergence had no significant effect (GLM: $F_{1,15}=2.56$, $p=0.11$). For all pups, weight at independence was significantly positively correlated with weight at one year (linear regression: $F_{1,27}=23.02$, $p<0.001$, $R^2=44.9$).

4. DISCUSSION

The results presented here show that banded mongoose helpers benefit the offspring that they care for in both the short and the long-term. Pups that spent a higher proportion of the pup care period with an escort were fed more, grew faster, were heavier at independence and were more likely to survive to three months of age than their littermates. Females that were heavier at independence also bred at a younger age. Within-litter comparisons showed that these effects were independent of group-specific variables, such as territory quality and group size, and environmental factors, such as rainfall and food abundance.

It is possible, however, that these results could be confounded by variation in the quality of offspring at the start of the feeding period. If pups compete for access to good helpers, then larger, high quality pups may be more likely to secure an escort. Some pups may also be growing faster than others regardless of the help that they receive. However, variation in initial pup weight is unlikely to explain the results presented here, as the positive effect of escorts on offspring success remained after controlling statistically for pup weight prior to the onset of the feeding period. Moreover, comparison of the same pup on days when it did and did not have an escort, confirmed that the presence of an escort on a given day significantly increased both the amount of food that pups received and their rate of weight gain, rather than some property intrinsic to the pup.

Identifying the mechanisms by which helpers benefit offspring is vital to understand fully the benefits that helpers gain (Innes & Johnston 1996; Hatchwell 1999). Helpers have been shown to reduce offspring mortality by decreasing predation (Rabenold 1990; Mumme 1992) and nestling starvation (Emlen & Wrege 1991), and to improve offspring growth through increased provisioning (Clutton-Brock *et al.* 2001). In the banded mongoose, the biomass of food fed to pups did not significantly improve their survival probability, which together with the observation that starvation is not a major cause of pup mortality, suggests that helpers improve pup survival by reducing the probability that they will be depredated. When predators approach, helpers actively defend the closest pup and carry it out of danger (Hodge 2003). As escorted pups generally have a helper close by, their predation risk will be significantly reduced. Pups that spent a higher proportion of the pup care period with an escort also grew faster and received more food items per hour, which suggests that their improved growth rate was a function of increased food intake. However, the biomass of food that pups received per hour was not a significant predictor of growth rate or weight at independence when escort index was included in the model, which suggests that increased provisioning is not the only mechanism through which escorts enhance pup growth. One explanation is that pups without an escort may lose more energy through begging and moving than their escorted littermates. Begging has been shown to be energetically costly in both birds (Leech & Leonard 1996; Kilner 2001) and mammals (White 2001), and begging rate commonly increases with increasing hunger levels (Kilner & Johnstone 1997). As escorted pups are fed more, it is likely that they are less hungry and consequently beg less. Pups with no escort also move greater distances between adults, which is likely to incur an energetic cost.

Females that were heavy at independence conceived at a younger age. As escorts increase pup weight at independence, this suggests that escorts can improve the future reproductive success of the female offspring for which they care. This has important implications for our understanding of cooperative breeding, as it suggests that helpers may benefit offspring in the long-term, and may, therefore, gain greater fitness benefits from helping than are currently assumed. While a positive effect of weight at independence on fecundity has been documented in several non-cooperative bird and mammal species (Lindstrom 1999), this has rarely been investigated in species that breed cooperatively. To date, the only other evidence comes from Solomon (1994), who found that weight at weaning had a positive influence on the future fecundity of female prairie voles (*Microtus ochrogaster*). While it is possible that the age at which females first breed could be influenced by initial differences in offspring size, I show the weight of the pup at emergence had no significant influence on age at first conception, suggesting that conditions experienced during the feeding period have a greater influence on future fecundity than those preweaning. As escorts increase both pup weight at independence, and the probability that they survive to breed, the effects of help on the future breeding success of offspring are likely to be substantial.

These findings provide strong evidence that banded mongoose helpers benefit the offspring that they rear. This has important consequences for the study of cooperative breeding, as it supports the assumption that helpers improve the reproductive success of breeders through their actions, not simply through their presence, and confirms that they have the potential to gain direct and indirect fitness benefits from helping. Furthermore, these results suggest that helpers can benefit offspring in the long-term, by improving their future fecundity. This raises the possibility that current studies substantially underestimate the fitness benefits that helpers are able to gain from rearing the offspring of others.

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