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Maternal weight, offspring competitive ability, and the evolution of communal breeding

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Despite the widespread occurrence of communal breeding in animal societies, the fitness consequences for mothers are poorly understood. One factor that may have an important influence on the net benefits mothers gain from breeding communally is the competitive ability of their offspring, as mothers are likely to gain substantial advantages from producing young who can outcompete the offspring of other females for access to resources. Here, we investigate the factors that influence offspring competition in the communally breeding banded mongoose (*Mungos mungo*). We show that heavy offspring are more likely to win competitive interactions with their littermates. Heavy offspring also receive more care and are more likely to survive to independence in large communal litters where competition is most intense. Our results also indicate that offspring weight at emergence is positively correlated with the weight of the mother at conception. As a consequence, the offspring of heavy mothers are likely to enjoy marked competitive advantages during early life. Together, our findings strongly suggest that the competitive ability of offspring will influence the costs and benefits that females experience while breeding communally and highlights the need for closer examination of the factors that influence offspring competitive ability and the influence this may have on the evolution of communal breeding. *Key words:* aggression, cooperative breeding, joint nesting, maternal effects, plural breeding, reproductive skew. *[Behav Ecol 20:729–735 (2009)]*

Communal breeding, where multiple individuals rear their young in a single nest or den and share parental care responsibilities, occurs across a diverse array of taxa (Brown 1987; Emlen 1991; Taborsky 1994; Solomon and French 1997; Hayes 2000; Vehrencamp 2000), but the fitness consequences of this behavior are poorly understood (Hayes 2000; Ebensperger et al. 2007). Potential benefits to be gained from communal breeding include improved thermoregulation, enhanced offspring survival, reduced maternal energy costs, and adoption of young should the mother die (Lewis and Pusey 1997; Cockburn 1998; Hayes 2000; Öst et al. 2002). However, rearing young communally could also involve costs for mothers, as offspring will have to compete not only with their own siblings for resources but also with the offspring of other females. The net benefits to be gained from communal rearing will therefore depend largely on the resources available to rear offspring and the ability of a female's offspring to compete for these resources should they be limiting (Hodge forthcoming). Differences in the competitive ability of offspring could therefore have a profound influence on the evolution of communal breeding and patterns of reproductive skew in animal societies, but as yet, we know little about the factors that influence the competitive ability of offspring in communally breeding groups.

Although relatively few studies have investigated offspring competition in species that breed communally, sibling competition has been well studied in parental care systems where offspring share the same mother (Mock and Parker 1997; Wright and Leonard 2002; Hudson and Trillmich 2008). In these species, young animals commonly beg, gape, jostle, and aggressively attack their siblings, and their success in competition depends on a variety of factors, including their hunger level and their size in relation to conspecifics (Mock and Parker 1997; Wright and Leonard 2002; Kilner and Drummond 2007; Hudson and Trillmich 2008). As differences in body size are also likely to give offspring a competitive advantage in communal systems, mothers who breed communally could gain substantial benefits from producing relatively large young who are likely to be superior competitors. For example, as older offspring will tend to be larger than their younger littermates, females are likely to gain advantages from producing young before their cobreeders, if this ensures that their own offspring will be older and hence superior competitors (Mennella et al. 1990). Mothers may also produce larger pups if they are large themselves and are therefore able to invest more in their offspring during gestation or accommodate larger offspring in their uterus (Clutton-Brock and Godfray 1991; Russell et al. 2003; Hodge et al. 2008). To investigate whether mothers are likely to benefit from influencing the competitiveness of their offspring, and to gain an understanding of the tactics they might use to do so, it is necessary to fully investigate the factors that promote successful competition among offspring in communally breeding species.

In this paper, we investigate the factors that influence the ability of pups to compete for care in the communally breeding banded mongoose (*Mungos mungo*) and ask whether maternal characteristics have the potential to influence offspring competitive ability. Banded mongooses are small (<2 kg) diurnal carnivores that live in stable groups of 8–40 individuals, which include multiple adult individuals of both sexes. Groups breed up to 4 times per year and during each breeding attempt up to 10 females (mean ± standard deviation [SD] = 3.75 ± 2.27) and give birth in synchrony to a communal litter that can contain up to 24 pups (mean ± SD = 6.69 ± 4.52). The communal litter spends the first 4 weeks of life in a natal

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den before joining the rest of the group on foraging trips. Until they are around 3 months of age (and able to forage independently), pups form associations with particular adults, termed "escorts" (Cant 1998), who provision their associated pup with food items and protect them from predators (Gilchrist 2004; Bell 2007; Gilchrist and Russell 2007; Hodge 2007). Escorts appear to feed the closest pup (Gilchrist 2004), and offspring aggressively defend escorts against approaches from littermates (Gilchrist 2008). Those pups that spend more time with exclusive access to an escort grow faster, have a higher probability of surviving to independence, and show enhanced reproductive performance in later life (Gilchrist 2004; Hodge 2005).

As banded mongoose pups gain substantial advantages from maintaining exclusive access to escorts, mothers are likely to benefit from producing highly competitive offspring that can successfully defend escorts against approaches by littermates. Variation in the competitive ability of banded mongoose pups is unlikely to arise through differences in offspring age, as pups within the communal litter are typically born on the same day (Cant 2000). However, pups show considerable variation in body weight when they first emerge from their natal den, and body weight may afford advantages in competition for escorts. Using behavioral and demographic data from a wild population of banded mongooses in western Uganda, we ask 3 specific questions. (1) Do heavy offspring have an advantage over smaller littermates when competing for escorts? (2) Are heavy offspring are more likely to survive to independence? (3) Do heavy mothers produce heavier pups than their lighter cobreeders?

METHODS

Study population and data collection

This study was conducted on a wild population of individually marked banded mongooses living in the Queen Elizabeth National Park, Uganda (0°12′S, 27°54′E). Details of habitat, climate, and study population are provided elsewhere (Cant 2000). Data were collected from 8 study groups between February 2000 and March 2002 and between May 2003 and September 2005. All individuals in the study population were habituated to the presence of observers, allowing the collection of behavioral data from within 2 m in 5 groups and from within 20 m in the remaining 3. Groups were visited approximately every 4 days to collect behavioral and life-history data, and in 5 groups, individuals were habituated to step onto a portable electronic balance, allowing regular body weights to be collected at the end of the day's foraging session without the need for capture (Hodge 2007). Permission to conduct this research was given by the Uganda National Council for Science and Technology, and research methods were approved by the Ugandan Wildlife Authority. All research protocols complied with the Association for the Study of Animal Behaviour Guidelines for the Use of Animals in Research.

To allow easy identification of individuals in the field, animals that had ceased growing were fitted with color-coded plastic collars (weighing ca. 1.5 g), and growing animals were marked by cutting a small area of their fur in a unique position (e.g., left leg, right shoulder, etc.). Collars and haircuts were maintained by trapping individuals every 3–6 months, although fur could be trimmed with scissors without the need for capture in well-habituated groups. Where necessary, individuals were captured in box traps (Tomahawk Live Trap Co, Tomahawk, WI) that were baited with a small amount of food (usually fish) and placed beneath dense bush to provide shade and protection. Traps were set at dawn and checked at regular intervals (maximum 2 h), either until the targeted group members had been captured or until 1600 h when traps were closed. Trapped individuals were anesthetized with an intramuscular injection of 1 mg/kg of ketamine (Vetalar: Veterinary Drug Co, York, UK) and 0.8 mg/kg of medetomidine (Domitor: Veterinary Drug Co). While under anesthetic, a small sample of skin (<2 mm) was taken from the tip of the tail and preserved in 10% salt–dimethyl sulfoxide for genetic analysis (Waldick et al. 2003). After processing (typically 10 min), captured animals were injected with 0.8 mg/kg atipamezole (Antisedan: Veterinary Drug Co) to reverse the effects of the medetomidine and placed in a covered trap to recover before being released at the trap site. This trap method was used 1107 times to trap 392 individuals with no casualties.

Each group contained between 1 and 13 females older than 1 year and hence of breeding age (mean ± SD = 5.40 ± 2.75). Most adult females (older than 1 year) in each group began to show behavioral signs of estrus (i.e., were closely guarded and mated by adult males within the group) within a week of one another, although older females typically came into estrus first (Cant 2000). On average, 68 ± 28% (mean ± SD) of adult females became pregnant and carried to term in each breeding attempt. Pregnancy lasts for 60–70 days in banded mongooses (Gilchrist 2006) and can be identified at around 30 days by swelling of the abdomen and an increase in body weight. Birth dates can be determined accurately by a sudden change in the female's weight and body shape. Pregnant females usually give birth on exactly the same day (Cant 2000), and offspring are reared in a communal litter.

Pups first begin foraging with the group at around 4 weeks of age (Gilchrist 2004). Until they can forage independently at around 12 weeks, they 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. During this "pup-feeding" period, we observed pups throughout the morning foraging session (for 3–4 h) and recorded the identity and distance to the nearest adult 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. Pups were only classified as having an escort if they spent more than 50% of the session close to the same individual as this excludes pups that were simply standing close to an adult at a given point in time but were not receiving care. Previous work has shown that the number of days that pups were classified as having an escort using this method has a positive influence on both their growth during the pup care period and their likelihood of surviving to 3 months of age (Hodge 2005).

We also conducted 20-min focal watches on pups during the pup-feeding period, during which time we recorded all competitive interactions over escorts between the focal pup and its littermates. Competitive interactions fell into 2 main classes of severity: "mild" aggression, where the aggressor either growled or briefly snapped at an approaching littermate, and "severe" aggression where 2 pups actively fought, grappled, or chased one another. For each competitive interaction, we recorded the identity of the competing pups, the initiator of the aggressive interaction, the identity of the "winner" if known (i.e., the pup that remained with the escort at the end of the interaction), and whether the winner was the original "owner" of the escort (i.e., whether the pup was with the escort before the competitive interaction took place).

Statistical analysis

Statistical analyses were performed in Genstat 6.1 (Lawes Agricultural Trust, Rothamsted, Harpenden, UK). As most analyses involved repeated sampling of individuals, litters, or groups, we used linear mixed models (LMMs) and generalized linear mixed models (GLMMs). These are similar to generalized linear models but allow both fixed and random terms to be included, with random terms taking into account repeated sampling (i.e., across individuals, litters, groups). Normally distributed data (confirmed by an Anderson–Darling normality test) were analyzed using LMMs with an identity link function, and binomial data were analyzed using GLMMs with a logit link function. In LMMs, variance components were estimated using the restricted maximum likelihood method, and GLMMs used penalized quasi-likelihood. Random terms were retained in the model unless variance components were found to be 0 (and hence, their removal did not change the findings reported). All potential explanatory terms were dropped sequentially until only those terms that explained significant variation remained. In all cases, repeating the analysis by successive inclusion of significant terms to build a minimal model from scratch yielded an identical final model. Once the minimal model had been established, each dropped term was then put back into the minimal model to obtain their level of nonsignificance and to check that significant terms had not been wrongly excluded. All 2-way interactions were tested, but results are only presented for those that were found to explain significant variation. All statistical tests were 2 tailed. Unless otherwise stated, means are quoted ± 1 standard error.

Are heavy pups more successful competitors?

To investigate patterns of aggression throughout the period of pup care, we took 513 focal watches conducted on 82 pups from 11 litters in 3 groups over 159 observation days. Whether or not the focal pup was involved in an aggressive interaction with a littermate during the 20-min focal watch was fitted as the binomial response term in a GLMM (1 = yes, 0 = no) with 1 as the binomial denominator. The age of the pup on the day of the focal watch (in days), pup sex, rainfall in the previous 30 days (mm), the number of littermates foraging on the day of the focal watch, and escort number on the day of the focal watch were included as potential explanatory terms. The date of the focal watch, litter identity, pup identity, and group identity were included as random terms. Pup and litter identity were nested within groups; random terms therefore had the following structure (date of the focal watch|group identity/litter identity/pup identity).

To determine whether heavier pups were more likely to win competitive interactions, we tested whether the difference between the weight of the winning and losing pup on the morning of a competitive interaction was significantly greater than 0. To avoid the possibility of "ownership" effects confounding results, we only included those interactions ($n = 59$ pups from 9 litters in 5 groups) where the winner was not the original owner. To determine whether heavier pups were more likely to associate with an escort, we fitted the number of days that 180 pups from 35 litters in 7 groups were in association with an escort as the binomial response term in a GLMM, with the number of days that association data were collected as the binomial denominator. This approach allowed the proportion of time pups spent with an escort to be investigated while controlling for variation in the number of observation days. Only pups for which more than 10 days of escort data were collected were included. The pup's weight at emergence relative to the litter average (g) was fitted as the main term of interest. Litter size at emergence, escort number, rainfall during the foraging period (30–90 days post birth), and pup sex were fitted as covariates. Litter and group identity were included as random terms, with litter identity nested within groups.

Do heavier pups show higher survival?

To determine whether heavy pups were more likely to survive to independence (3 months), we fitted whether or not 131 pups from 28 litters in 7 groups survived (1 = yes, 0 = no) as the binomial response term in a GLMM, with 1 as the binomial denominator. Relative pup weight was included as the main term of interest as in the analysis of time spent with an escort above. Litter size at emergence, escort number at emergence, rainfall (during the foraging period 30–90 days post birth), and pup sex were fitted as covariates. Litter and group identity were included as random terms, with litter identity nested within groups.

Do heavier mothers produce heavier pups?

As pups are usually born synchronously in an underground communal den, assignment of maternity requires genetic analysis. DNA was extracted from tissue samples using Chelex bead extraction and Qiagen tissue extraction and genotyped at 12 polymorphic microsatellite loci using the methods described in Waldick et al. (2003). We used the program Cervus (Marshall et al. 1998) to assign maternity and included all females who were known to be pregnant prior to the birth of the litter as candidate mothers. To assess whether a mother's weight influenced pup weight at first emergence from the natal den (between 25 and 31 days of age), we used only those pups who could be assigned to mothers with a confidence of more than 90%. We fitted the weight of 39 such pups from 15 litters born to 13 mothers in 5 groups as the response term in an LMM. Mother's mean weight (g) in the 60–70 days prior to birth (i.e., the period around conception) was fitted as the main term of interest, and the age of the pup at first weighing (days), total rainfall during gestation (60 days pre birth), litter size at emergence, and escort number at birth (all group members > 6 months) were tested as covariates. Given the small sample size, we did not include pup sex as a covariate in this model, as previous work has shown that male and female pups do not differ in weight (Hodge 2003, 2005). Litter, group, and mother's identity were included as random terms, with litter identity nested within group identity. Random terms therefore had the following structure, mother's identity|group identity/litter identity.

RESULTS

Are heavier pups more successful competitors?

Pups competed aggressively for access to escorts. On average (±SD), pups were involved in 3.42 ± 4.19 competitive interactions over escorts per hour during the first 2 weeks that they foraged with the group. The probability that a pup was involved in competition with a littermate during a focal watch was highest when pups first began foraging with the group and declined as pups aged (Figure 1a, Table 1). Competitive interactions were also more likely in large litters (Table 1) and when there were few escorts in the group (Figure 1b, Table 1). The majority of aggressive interactions (85%) were classed as "mild," where one pup briefly snapped and lunged at an approaching littermate, causing it to retreat, but 15% of interactions involved a full fight, where the competing pups grappled and chased one another.

Pups that won competitive interactions over escorts were significantly heavier than those that lost (winner weight: 236 ± 6 g, loser weight: 219 ± 5 g; paired t-test: $t_{58} = 2.75$, $P = 0.004$). Probably, as a consequence of this success in competition, heavy pups spent 16% more time with an escort than relatively light pups in large litters (of >8 pups) when competition for escorts was most intense. In small litters, however (<8 pups), pup weight had no influence on the amount of time that pups spent with an escort (Figure 2a, Table 2).

Do heavy pups show higher survival?

Pup mortality was high in our study population, and 57.4 ± 35% (mean ± SD) of emergent pups died before they reached

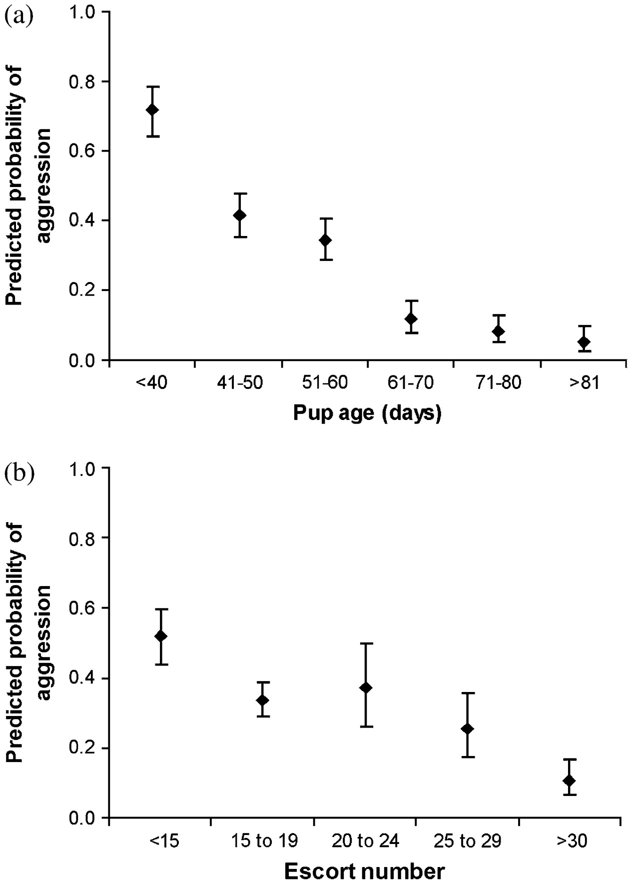

Figure 1
The influence of (a) pup age and (b) escort number on the probability that a pup would be involved in an aggressive interaction during a 20-min focal watch. Figures show predictions from a GLMM controlling for litter size and repeated measures within focal date and group litter and individual identity.

3 months of age. Heavy pups were significantly more likely to survive to independence than light pups in large litters, but in small litters their survival probability did not differ (Figure 2b, Table 2).

Table 1
Factors affecting the probability of pup competition (GLMM)

	Probability of pup competition (g)		
Explanatory terms	Estimate ± standard error	Wald statistic (χ^2)	P
Pup age (days)	−0.078 ± 0.011	42.23	**<0.001**
Escort number on day of focal watch	−0.092 ± 0.029	10.15	**0.002**
Communal litter size	0.091 ± 0.043	4.56	**0.037**
Rainfall 30 days prefocal (mm)	−0.00011 ± 0.0041	0.00	0.98
Pup sex			
Female	0.0 ± 0.0	0.53	0.47
Male	−0.20 ± 0.27		
Constant	−2.21 ± 1.19		

Significant terms are highlighted in bold. Focal date (component ± standard error = 0.69 ± 0.29), group identity (3.04 ± 4.03), litter identity (0.0 ± 0.0), and pup identity (0.034 ± 0.15) were included as random terms.

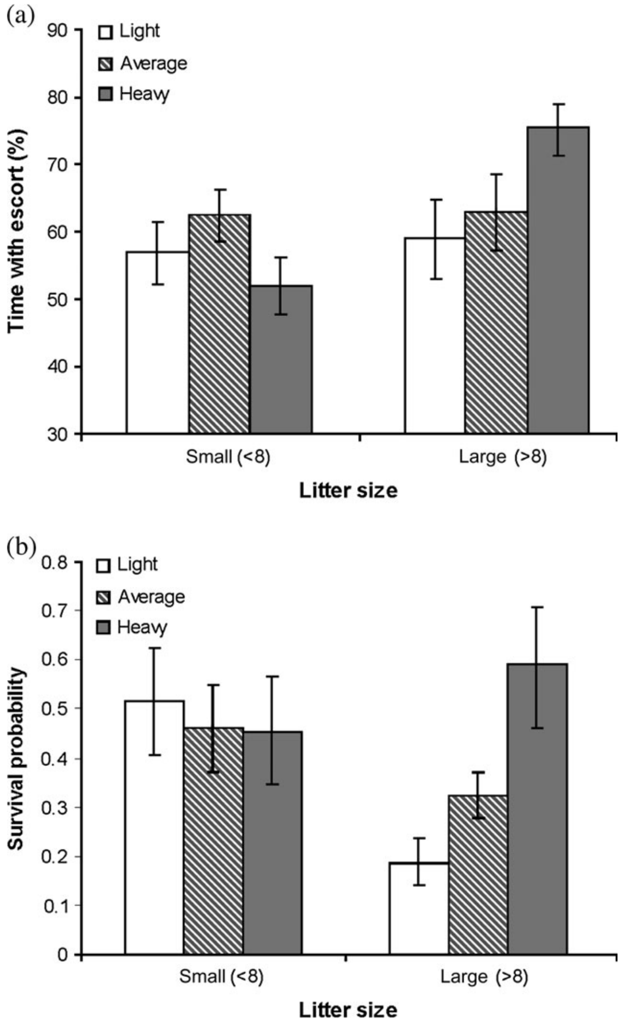

Figure 2
The influence of pup weight on (a) the proportion of time spent with an escort during the pup-feeding period and (b) the probability of surviving to independence (3 months) in large (≥8) and small (<8) litters. Figures show predictions from a GLMM controlling for repeated measures within litters and groups. Pups were classified as "heavy" if they were more than 10 g heavier than the litter mean, "average" if they were within 10 g of the litter mean, and "light" if they were more than 10 g lighter than the litter mean.

Do heavier mothers produce heavier pups?

Pups varied considerably in weight when they first emerged from the natal den, ranging from 70 to 248 g ($n = 206$ pups). This variation was extreme even within litters, with the largest pup in the litter 1.5 ± 0.5 (mean ± SD) times larger than the smallest pup on average and up to 3 times heavier in some litters. After controlling for positive effects of age at emergence and litter size (Table 3), mother's weight at conception had a strong positive influence on pup weight at emergence (Table 3, Figure 3). There was no additional influence of a mother's age at conception when her weight was included in the model (Table 3).

DISCUSSION

Our results demonstrate that heavy banded mongoose pups have an advantage when competing with their littermates for access to escorts. Heavy pups spend more time with escorts in large communal litters, where competition for escorts is

Table 2

Factors affecting the proportion of time pups spent with an escort (GLMM) and their probability of surviving to 3 months (GLMM)

	Time with escort (%)			Probability of survival to 3 months		
Explanatory terms	Estimate ± standard error	Wald statistic (χ^2)	*P*	Estimate ± standard error	Wald statistic (χ^2)	*P*
Relative weight ×litter size	See Figure 2a	4.46	**0.037**	See Figure 2b	4.28	**0.039**
Relative weight	See Figure 2a	4.12	**0.045**	See Figure 2b	4.73	**0.030**
Communal litter size	See Figure 2a	7.57	0.013	See Figure 2b	0.00	0.90
Rainfall (mm)	−0.0027 ± 0.0019	2.23	0.15	−0.0088 ± 0.0048	3.33	0.07
Pup sex						
Female	0.00 ± 0.00	0.44	0.51	0.00 ± 0.00	0.92	0.34
Male	−0.10 ± 0.15			0.30 ± 0.32		
Escort number at emergence	−0.012 ± 0.013	0.82	0.32	0.025 ± 0.029	0.75	0.39
Constant	0.48 ± 0.084			0.23 ± 0.26		

Significant terms are highlighted in bold. Relative weight refers to the weight of the pup at first emergence from the natal den relative to the litter mean. Group identity (component ± standard error = 0.0 ± 0.0 for time with escort and 0.0 ± 0.0 for probability of survival) and litter identity (0.036 ± 0.048 for time with escort and 1.44 ± 0.58 for probability of survival) were included as random terms.

most intense, and have a higher probability of surviving to independence. As a mother's weight at conception has a positive influence on the weight of her pups at emergence, the offspring of heavy females are therefore likely to enjoy marked competitive advantages during early life. Together, our findings suggest that the net fitness benefits that banded mongoose females accrue while breeding communally will be influenced by their weight at conception as heavy females are likely to produce offspring that have a competitive advantage over their littermates when escorts are limiting.

Although our results indicate that heavy pups spend almost 80% of their time with escorts in large litters (20% more than their lighter littermates), they spend only 50% of their time with an escort in small litters. This finding is somewhat surprising, as all pups might be expected to spend a large proportion of time with an escort in small litters, where the availability of escorts is unlikely to be limiting. This finding probably reflects differences in the benefits of having a permanent escort in litters of different size. In large litters, where competition between pups is intense, pups need to remain close to a helper at all times to ensure that they are fed and that they are protected if a predator approaches. In small litters, however, where there are a fewer pups to "deplete" potential feeders, pups may be able to gain more food from moving between different escorts than from remaining close to just one (Hodge et al. 2007). In addition, when there are few pups in the group, the likelihood that unescorted pups will be left behind when a predator approaches will be lower, which is likely to explain why all pups show relatively high survival in small litters, regardless of their body weight.

As heavy females are likely to produce pups who are superior competitors when escorts are limiting, mothers may be under strong selective pressure to maintain body condition throughout conceptive periods. This may help to explain, in part, why female banded mongooses invest less than males in cooperative activities during times when they are likely to conceive. Female banded mongooses typically conceive shortly after giving birth (Cant 2000; Gilchrist 2006), and as investment in offspring care in this species results in weight loss (Hodge 2007), females who invest heavily in cooperative activities at this time are likely to give their unborn offspring a competitive disadvantage when competing for escorts in the future. The importance of maternal weight at conception also raises the exciting possibility that mothers in communally breeding groups may benefit from controlling the weight of other group members (e.g., by restricting their access to food

Table 3

Factors affecting pup weight at emergence (LMM)

	Pup weight (g)		
Explanatory terms	Estimate ± standard error	Wald statistic (χ^2)	*P*
Mother's weight at conception	0.13 ± 0.041	10.22	**0.004**
Communal litter size	5.48 ± 2.38	5.28	**0.042**
Age at emergence (days)	10.85 ± 1.87	33.53	**0.001**
Rainfall during gestation (mm)	0.13 ± 0.17	0.58	0.46
Escort number at birth	−1.22 ± 1.18	1.07	0.34
Mother's age at conception (months)	−0.23 ± 0.53	0.19	0.67
Constant	189.8 ± 13.55		

Significant terms are highlighted in bold. Group identity (component ± standard error = 462.4 ± 675.9), mother identity (420.9 ± 451.0), and litter identity (166.5 ± 302.8) were included as random terms.

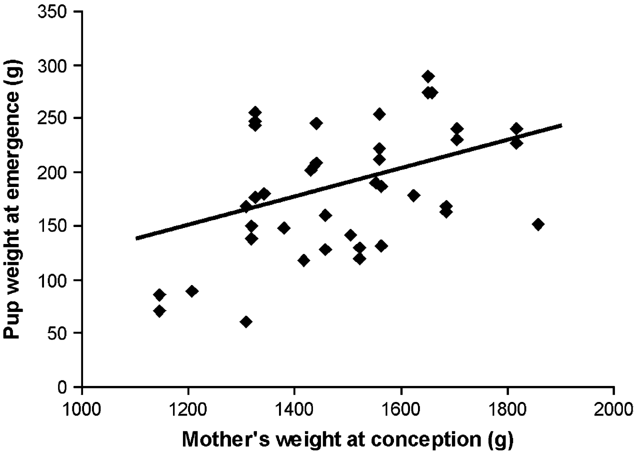

Figure 3

The influence of mother's weight at conception on the weight of pups when they first emerge from the natal den (n = 39 pups). Figure shows raw data alongside the fitted line from an LMM controlling for pup age and litter size and repeated measures within mothers, litters, and groups.

sources or evicting females from the group if they grow too large). Although to our knowledge, this has not been investigated in a communal breeder, there is evidence that some coral reef fish evict subordinates if their length exceeds a particular threshold, which results in subordinates regulating their growth to ensure that the size differential between females remains sufficiently large (Wong et al. 2007).

In addition to strategically maintaining their own body weight at conception, mothers in communally breeding groups could manipulate the competitive ability of their young in other ways. In Norway rats (*Rattus norwegicus*) and meerkats (*Suricata suricatta*), for example, younger pups compete less effectively for care than their older siblings, which means that females stand to gain substantial advantages from ensuring that they give birth earlier than their cobreeders (Mennella et al. 1990; Hodge SJ, unpublished data). This may explain why dominant female meerkats kill offspring born before their own but allow litters born after their own to survive (Clutton-Brock et al. 2001; Young and Clutton-Brock 2006) and may also help to explain why several species of communally breeding birds toss eggs laid before their own from the nest (e.g., groove-billed anis, *Crotophaga sulcirostris*, Vehrencamp 1977; acorn woodpeckers, *Melanerpes formicivorus*, Mumme et al. 1983; guira cuckoos, *Guira guira*, Macedo et al. 2001; smooth-billed anis, *Crotophaga ani*, Schmalz, Quinn, and Lentz 2008).

Mothers may also be able to manipulate the competitiveness of their offspring by adaptively adjusting their offspring's growing environment (Mousseau and Fox 1998; Russell and Lummaa 2009). There is now good evidence that avian mothers can adjust the competitive ability of their offspring by manipulating the nutritional content of the egg (Cunningham and Russell 2000) or adjusting yolk androgen levels (Gil 2003; Groothuis et al. 2005). Although few studies have investigated the influence of these kinds of maternal effects in communal breeders, there is some evidence that yolk androgens increase with female number, and hence the competition that offspring are likely to face, in the communally breeding guira cuckoo (Macedo et al. 2004). No such effect was found in another communally breeding bird, the smooth-billed ani, however (Schmalz, Quinn, and Schoech 2008).

Our findings suggest that the costs and benefits that females experience while breeding communally will be strongly influenced by the competitive ability of their offspring. This could have important consequences for our understanding of the evolution of communal breeding, influencing not only when females breed communally but also who they choose to breed with and how they behave in communally breeding groups. As such, differences in the competitive ability of young could have an important influence on our understanding of the factors that influence variation in reproductive skew in general. Most empirical investigation of reproductive skew to date has focused on testing the predictions of theoretical models that assess the factors influencing the costs and benefits that dominants experience when subordinates breed (Keller and Reeve 1994; Johnstone 2000; Hager 2003; Magrath et al. 2004). Our findings suggest that these costs and benefits may be strongly influenced by the competitive ability of offspring, as if dominant females produce offspring that are superior competitors (perhaps because they are larger, more aggressive, or give birth earlier), they may suffer fewer costs when subordinates breed, reducing the need for reproductive suppression (Hodge forthcoming). We suggest that new insights into the evolution of communal breeding and reproductive skew are likely to arise from empirical work that investigates whether the offspring of different females vary in their ability to compete for resources and whether mothers are able to manipulate offspring competitive ability, as well as theoretical work that explores the impact of such differences on stable levels of reproductive skew.

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