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Why breed communally?
Factors affecting fecundity in a communal breeding mammal:
the banded mongoose (*Mungos mungo*)

Abstract Fecundity is an important component of fitness. In cooperatively breeding species, studies aimed at understanding the factors that affect fecundity have largely been restricted to species that exhibit high reproductive skew, where reproduction is monopolised by a few individuals. In such species, dominant suppression and inbreeding avoidance are the principal explanations for low fecundity in subordinate females. In this paper, we evaluate the relative effects of individual, social, and environmental factors on female fecundity in a low skew cooperative breeding mammal: the banded mongoose (*Mungos mungo*). Most females (80%) conceived in each breeding event, and most pregnant females (93%) carried their litter to term. The principal determinants of a female's fecundity were intrinsic qualities, particularly age and body size. However, there was no evidence of dominant suppression of subordinate reproduction or inbreeding avoidance. Similarly, there was little indication that social or environmental factors influence fecundity. We suggest that in the banded mongoose, the apparent lack of costs to inbreeding, and the absence of dominant female suppression of reproduction in other females result in low reproductive skew. Indeed, in banded mongooses, like lions (*Felis leo*), multiple breeding may be a consequence of benefits to rearing young communally.

Keywords Cooperative breeding · Egalitarian · Plural breeding · Reproductive skew · Reproductive success

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Introduction

Social groups in which there is an uneven distribution of reproduction between group members are said to exhibit reproductive skew. Reproductive skew, and the factors that affect it, has provoked much theoretical and empirical interest (Keller and Reeve 1994; Clutton-Brock 1998; Johnstone 2000; Clutton-Brock et al. 2001a). One reason for this is that the degree to which dominant individuals monopolise reproduction varies considerably between species (Keller and Perrin 1995). However, despite this variation, the majority of vertebrate studies have examined the factors that affect the probability and success of reproduction in species exhibiting high reproductive skew, where one or two individuals reproduce to the exclusion of others (Emlen 1997; Lewis and Pusey 1997, for examples see Stacey and Koenig 1990; Solomon and French 1997). The aim of this study is to investigate the factors that affect female fecundity in a cooperative breeding mammal with low reproductive skew, the banded mongoose (*Mungos mungo*).

High skew cooperative breeders are defined by monopolisation of reproduction by a limited number of individuals. The two principal hypotheses for the apparent 'reproductive suppression' of subordinates are: (1) dominant control of subordinate reproduction (Creel et al. 1992; Clarke and Faulkes 1997; Creel and Waser 1997); and (2) a lack of access to unrelated partners (Koenig et al. 1998; Cooney and Bennett 2000; O'Riain et al. 2000;

Faulkes and Bennett 2001). For 'suppressed' females, these translate into: (1) losing out to competition with a larger or more formidable female; or (2) postponing reproduction due to a lack of access to unrelated males. Whilst dominant suppression is usually related to body size, with larger females suppressing reproduction in smaller females (e.g. Creel and Waser 1991; Faulkes and Abbott 1997; Clutton-Brock et al. 2001a), inbreeding avoidance occurs in the absence of unrelated males (e.g. Reyer et al. 1986; French 1997; O'Riain et al. 2000; Faulkes and Bennett 2001). In general, suppression of reproduction by dominant females and reproductive restraint due to inbreeding avoidance occur at the pre-parturition stage (e.g. Creel et al. 1992; Faulkes and Abbott 1997; French 1997; Clutton-Brock et al. 2001a).

A common assumption of reproductive skew models is that dominant females benefit from suppressing subordinate reproduction. This assumption predominates because in species that exhibit high reproductive skew, positive relationships between helper number and productivity of dominant females are common (Jennions and Macdonald 1994; Emlen 1997). Additionally, Russell et al. (2003) have shown for cooperatively breeding meerkats (*Suricatta suricata*) that the fecundity of dominant females increases with the number of helpers. However, dominant reproductive success need not increase by suppressing subordinate reproduction, and subordinate reproduction can even be beneficial to dominants in species with low reproductive skew (Packer et al. 2001).

The banded mongoose is a low skew communal breeder, in which up to ten females breed synchronously (Gilchrist 2001). Banded mongooses are small (<2 kg) insectivorous group-living mammals that live in equatorial Africa. Within groups, females come into behavioural oestrus approximately synchronously, and give birth approximately synchronously in the same den (Cant 2000). Although dominant males attempt to exclude other males from mating by mate guarding, females usually copulate with multiple males within their group during oestrus periods (Cant 2000). On average, a female breeds 3.79 ± 0.14 ($n=56$ females) times a year (Gilchrist 2001).

Female banded mongooses exhibit characteristics that, according to traditional theoretical models of reproductive skew (Keller and Reeve 1994), should dispose them toward high reproductive skew: group-living females gain higher per capita reproduction than do solitary females, dispersing females suffer reduced fitness (at least in the short-term), and female group-mates are always close genetic relatives (Gilchrist 2001). Yet banded mongoose groups almost always contain multiple breeding females. Whilst the presence of multiple breeding females suggests that there is less inter-individual variation in fecundity than in species with high reproductive skew, there may still be appreciable variation between individuals in components of fecundity. In cooperative breeding species with low reproductive skew, the factors that affect fecundity and variation in fecundity between individuals require investigation. In this paper, we evaluate how individual, social and environmental factors affect fecundity in wild banded mongooses in Uganda. Does fecundity increase with age, body size or dominance? Is fecundity diminished when females are in a group with only related males? Does fecundity increase with the number of carers in the group, or decrease with group size? In addition, we evaluate the effects of body condition, number of breeding females and food availability, factors that commonly affect vertebrate fecundity (Clutton-Brock 1988).

Methods

Study area and population

Fieldwork was carried out in an 8-km^2 area, on and around Mweya peninsula, Queen Elizabeth National Park, southwest Uganda 0°12′S and 27°54′E, from March 1997 to February 2000. The vegetation of the study site was predominantly short and medium fire climax grassland with numerous dense thickets dominated by *Capparis tomentosa* growing in association with *Azima tetracantha* and *Euphorbia candelabrum* (Lock 1977). The climate was equatorial, with little annual fluctuation in day length or temperature.

Data were collected on 79 female banded mongooses, in 15 groups, producing 70 group-litters over 3 years. Three of the groups had access to supplemental food from human garbage dumps (Gilchrist and Otali 2002; Otali and Gilchrist 2004). Groups are referred to as non-refuse-feeding or refuse-feeding, indicating their access to supplemental food. Social and environmental variables are summarised in Table 1.

Data collection

Body size and condition

Individuals were trapped, anaesthetised, marked and located using methods outlined previously (Cant 2000; Cant et al. 2001). Adult females were trapped on average 5.09 ± 0.36 times during the study. Anaesthetised animals were weighed (±0.5 g), and head width (zygomatic arch breadth ±0.1 mm) measured. We used a residual index to measure body condition (Jakob et al. 1996). Log body mass was regressed on log head-width and the equations for the line of best fit were used to calculate predicted body mass for each capture (excluding pregnant females). Body condition index was calculated as observed body mass ÷ predicted body mass, which has a mean of 1. All biometric measurements (including foetus counts and estimates of foetus size) were made by one observer (JSG).

Pregnancy status, foetus number and size, and abortion

By trapping and anaesthetising females 2–4 weeks after oestrus (gestation is approximately 8 weeks; Cant 2000), it was possible to detect pregnancy, count the number of foetuses, and estimate the size of foetuses (on a scale of 1 to 8), by gentle palpation. Trapping and palpating pregnant females did not effect the probability that they aborted ($\chi^2=2.37$, $df=1$, $p=0.13$, $n=264$). For females that were not trapped, pregnancy was evident from the fourth week of gestation, as females had a visibly swollen abdomen. Parturition or abortion was detected when the abdomen size returned to normal. If a female conceived and aborted prior to trapping, and early in the gestation period (before 3 weeks gestation), then she could have been mis-classified as a non-conception, rather than as an abortion. This is unavoidable, and common to the majority of field studies considering conception frequency. However, this does not represent a major problem to either the results or conclusions of the paper,

Table 1 Variables used as fixed effects in models of fecundity of banded mongooses (*Mungos mungo*)

Variable	Summary[a]: mean (range)
Individual	
Age (days)[b]	883 (230–2,209)
Reproductive experience[b]	Not given birth / previously given birth
Head-width (mm)	42.7 (39.1–45.9)
Body weight (g)	1,387 (1,000–1,740)
Body condition	1.0 (0.87–1.19)
Conception status for the previous litter[c]	Barren / gave birth
Parturition status for the previous litter[c]	Barren / gave birth
Abortion status for the previous litter	Full gestation / aborted
Oestrus status	Not mate guarded / mate guarded
Oestrus order	1 (first) to n (last)
Rank	1 (highest) to n (lowest)
Access to unrelated ♂s in group	Natal males only / non-natal males present
Social	
Group size	19.6 (4–36)
No. of reproductive ♀s[d]	6.2 (1–10)
No. of pregnant ♀s[d]	4.9 (1–10)
Carer number[e]	15.0 (0–22)
♂ carer number[e]	9.0 (0–18)
Pup no. at oestrus	1.8 (0–16)
Success to emergence of previous litter	Failed / emergent
No. emergent pups from previous litter	4.7 (0–17)
Proportion of ♀s with access to unrelated ♂s	0.42 (0–1)
Environmental	
Access to refuse	Non-refuse / refuse
Proportion of days with rain[f]	0.29 (0.02–0.63)
Rainfall: mean daily rain[f]	2.2 (0.0–5.4)

[a] Values given for reproductive females (females that had conceived previously or were conceiving for the first time).

[b, c, d, e, f] In each case, the two terms were not included in models together due to collinearty: the more significant term was retained

[f] Within 60 days pre-conception

because both non-conception and abortion indicate a failure to breed, and therefore similarly affect the overall level of skew.

Rank and oestrus order

Females rarely show aggression. We therefore assigned females a rank in two ways: (1) according to the order in which they were mate guarded by a male during the group oestrus event in which conception occurred ('oestrus order'); and (2) a combination of oestrus order and the dominance rank of the male ('dominance rank'). These measures are likely to be associated with 'true' rank because the order in which females are mate-guarded is generally positively correlated with their age, and mature females are usually guarded by the highest-ranking males (Cant 2000). Males compete aggressively for females during oestrus, and we calculated a linear dominance hierarchy for males based upon dyadic displacements and repulsions between males in competition for females during oestrus. For oestrus order, the first female to be mate-guarded was given the highest rank 1; the second female to be mate-guarded was given the next rank 2, and so on. For dominance rank, we ranked females that were tied for oestrus order according to the rank of the male that mate guarded each. The female mate guarded by the top male was given the highest rank within the tie 1, the female mate-guarded by the next highest ranked male was given the next rank 2 and so on.

Access to unrelated males

Group history was known from 1994, and in no case did an individual immigrate into an established group (Cant et al. 2001; Gilchrist 2001). Therefore, females that conceived within their natal group did not have access to 'unrelated' males within the group, and females that conceived within a group formed by fusion of male and female subgroups from different natal groups had access to 'unrelated' males within the group.

Whilst females could have mated with extra-group males, the incidence of such matings was rare, especially relative to the frequency of matings with males within the group (J.S. Gilchrist, unpublished data). Opportunities for extra-group copulation were almost exclusively limited to inter-group encounters (females rarely independently left the group). In over 615 h of observations on groups in oestrus (n=58 group-oestrus events in 11 groups) we witnessed only 15 inter-group encounters (where extra-group copulation could have occurred). Sexual behaviour was witnessed in only 6 of these 15 inter-group encounters. The relatively low incidence of successful extra-group copulations relative to within-group copulations is supported by genetic data (R.C. Waldick, J.S. Gilchrist, S. Hodge, B. Amos, unpublished work).

Group size and number of carers

Group size was calculated as the number of individuals over 90 days of age. All group members over 6 months are capable of contributing care to the communal litter (Gilchrist 2001). We therefore calculated the number of carers as the total number of group members over 6 months of age. As males tend to make higher contributions than females to care through both babysitting and escorting (Rood 1974; Gilchrist 2001, 2004), we additionally calculated the number of male carers.

Statistical analysis

For analyses, we divided fecundity into its components: age of first conception, probability of conception, group inter-conception interval, litter size, foetus size, and probability of abortion. Unless

stated otherwise, in each analysis we fitted individual, social and environmental variables (see Table 1) as fixed effects.

Statistical analyses were performed using GenStat 5.4.1. Normally distributed data were analysed using Restricted Estimate Maximum Likelihood Models (REML). Binomial data were analysed using Iterated Reweighted Restricted Maximum Likelihood Models (IRREML), a robust form of Generalized Linear Mixed Model, with logit link function and binomial error distribution. REML and IRREML models enable fitting of random terms and therefore account for repeated sampling across error terms (Schall 1991): groups, litters and individuals. The random terms: group identity, litter identity and individual identity were dropped from a model when identified as a negative component of variance (indicating that they explain none of the variance in the model). A General or Generalized Linear Model procedure was used when all random terms were dropped from a model. Dispersion was estimated in all models, with the exception of the conception probability, foetus count and abortion analyses where the data were under-dispersed, and dispersion was fixed at 1.

Due to inter-correlation between individual (biometric and oestrus behavioural) effects, each individual effect was tested independently (alone in the model with no other fixed effects). Where individual effects were significant, the most significant effect was retained for analyses of social and environmental effects, and the forward stepwise procedure was then used in selecting fixed effects for the minimal model (Sokal and Rohlf 1995). The minimal model comprised only those parameters that contributed a significant amount to the explanatory power of the model. Wald statistics for each significant fixed term were derived from each term fitted last in the minimal model with all significant terms in the model together, whereas values for non-significant terms were calculated from the minimal model with only that non-significant term added last. Relevant two-way interactions were tested (in the presence of the main effects) but are not included in Results unless significant. Wald statistics were evaluated using the χ^2 distribution (as is appropriate for large datasets, e.g. Kruuk et al. 1999; Clutton-Brock et al. 2001a). Results were consistent on confirming against the most conservative method: using the F-distribution with denominator degrees of freedom equal to the number of units in the highest significant random stratum (Elston 1998). The significance level was $\alpha < 0.05$. All means are expressed as ± 1 SE.

Age at first conception

Twenty-five females ($n=12$ cohorts, 5 groups) that were born during the study period also conceived their first litter during the study period. The effects of individual characteristics on age of first conception were tested by comparing biometric data between the non-reproductive and primiparous cohort members within each litter where some (but not all) cohort members conceived for the first time. There were five cohorts (in three groups) where females born within the same litter conceived their first litter at different ages, and the entire cohort was trapped on the same day, within 32 days of the date of first conception. Conception status (for the litter) of each cohort member that had not previously conceived (did not conceive =0, conceived =1) was fitted as the fixed effect in a REML model with body weight, body size or body condition as the response variate. The litter in which the first conception(s) occurred was fitted as the random term.

Social factors were calculated as the mean values over the three oestrus events prior to the female reaching 230 days (the minimum confirmed age of conception). For rainfall, we calculated the values over the 150 days (the average interval between three oestrus events) prior to 230 days old. Social and environmental terms were fitted as fixed effects in a GLM with age at first conception as the response variate.

Conception probability

Data on conception in reproductive females (females that had previously conceived or were gestating their first litter) was available from 339 potential conceptions, from 81 females, 69 litters and 11 groups. Within each communal litter, each female was scored for conception as: not pregnant =0, pregnant =1. In addition to other individual terms, we tested whether a female's body size relative to the largest female conceiving for the litter was a predictor of conception probability using relative head-width [(head-width of largest female – head-width of female) / head-width of largest female]. This index was only calculated for litters where all females had head-width measured (65 females, 19 litters and 10 groups). Individual, environmental and social variables were fitted as fixed effects in an IRREML model with binomial error structure in which conception was fitted as the response variate with binomial denominator 1. Litter identity was fitted as the random model.

Inter-conception interval

Group inter-conception interval was used rather than female inter-conception interval because all females within a group generally conceived and gave birth within a few days of each other, and differences between females (within groups) were more appropriately analysed as failure to conceive or failure to gestate to full term. Therefore individual effects were not fitted in this model. Group inter-conception interval was calculated as the time in days from the first recorded date of conception of one communal litter to the first recorded date of conception for the subsequent communal litter ($n=57$ litters, 11 groups). The date of conception was taken as 63 days prior to the date of first parturition (Cant 2000). For asynchronous litters, the first sub-litter for each communal litter was used. Only litters for which date of parturition was known to an accuracy of at least 7 days were included in the analysis. Group inter-conception interval was log transformed (base 10) to normalise the data, and analysed using GLM. Social and environmental terms were fitted as fixed effects. Social variables were recorded at the parturition event preceding the inter-conception interval. Environmental variables were recorded within the inter-conception interval.

Foetus count and size

Analysis of foetus count (litter size) includes only females that were pregnant when trapped. There were 197 foetus counts from 77 females, 62 litters and 15 groups. Analysis of foetus size was based upon one value per female per litter, taking the median foetus size estimation (within a female, foetuses were usually of the same size class; J.S. Gilchrist, unpublished data). Within each litter, we included females palpated within no more than 5 days of each other. Analysis used GLM, fitting foetus count to a Poisson distribution. Individual, social and environmental terms were fitted as fixed effects.

There were 157 foetus size measurements from 71 females, 44 litters and 13 groups. We investigated which factors affected foetus size within communal litters using a REML model, by modelling individual factors only. Access to unrelated males was not included because it did not vary within litters. Environmental and social variables were not included because analysis of variation in foetus size between litters could not control for differences in duration of gestation. Litter identity was fitted as the random term.

Abortion probability

We investigated the factors affecting the probability of a female failing to carry her litter from conception to parturition. Data on abortion was available from 265 conceptions, from 68 females, 70 litters, and 11 groups. Within each communal litter, each female was scored for abortion as: did not abort =0, aborted =1. Individual,
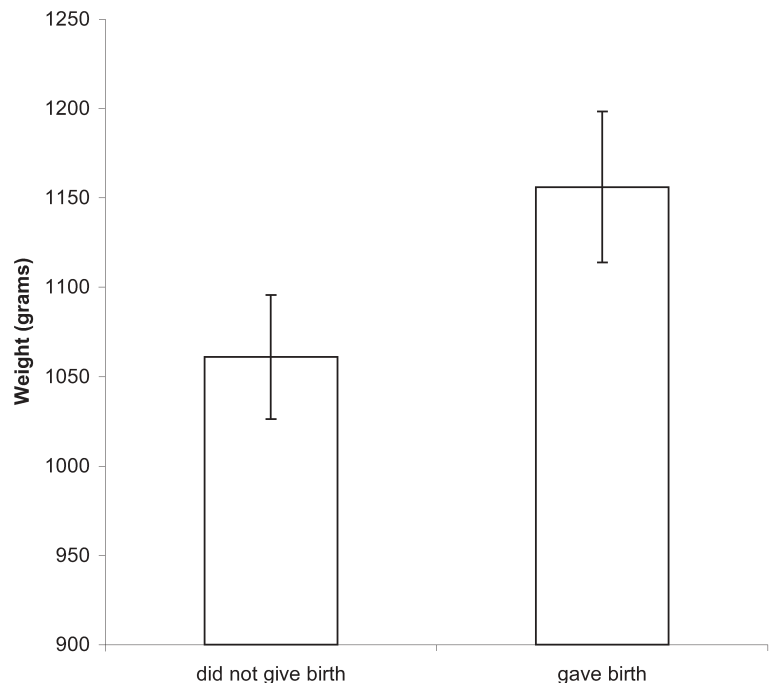
environmental and social variables were fitted as fixed effects in a GLM model with binomial error structure in which abortion was fitted as the response variate with binomial denominator 1.

Results

Age at first reproduction

Age at first conception was affected by individual, social and environmental factors. The mean age at first conception was 321±8.72 days (range 230–385). Within a cohort, larger females conceived their first litter at a younger age than smaller females (head-width: χ^2=3.96, df=1, p0.047, n=25; body weight: χ^2=4.00, df=1, p=0.046, n=26, Fig. 1). Body condition did not differ between females that conceived for the first time and cohort members that did not conceive. Females did not avoid or delay reproduction with access to only related males within their group: all 25 females that conceived their first litter during the study period did so within their natal group, and all females that emigrated had previously conceived within their natal group (24 females in 7 permanent emigration events, and 11 females in 4 temporary emigration events). There was no effect of carer number or group size on age of first conception. However, females conceived their first litter earlier in groups with more reproductive females ($F_{1,21}$=10.1, p=0.005, n=24; Fig. 2a). Age at first conception also increased with rainfall in the 5 months prior to the earliest date of conception ($F_{1,21}$=10.5, p=0.004, n=24; Fig. 2b).

Conception probability

The probability of conception was not affected by individual and environmental factors, but was affected by previous reproduction. There were 273 conceptions and 62 non-conceptions. Twenty-five of the conceptions were first conceptions and eight were to immigrant females (conception history unknown). Therefore conception rate for parous females was 79.5%. There was no correlation between the probability of conception and age, head-width, head-width relative to the largest female, body weight, or body condition. Whilst females that were mate-guarded during oestrus were marginally more likely to conceive (χ^2=2.85, df=1, p=0.091, n=210), amongst females that were mate-guarded there was no relationship between probability of conception and either rank or order of oestrus. There was no evidence that conception was affected by access to unrelated males within the group. Additionally, there was no effect of carer number, group size, number of reproductive females, rainfall, or access to refuse. However, the likelihood that a female conceived decreased with the success of the previous communal litter (measured as the number of emergent pups: χ^2=7.07, df=1, p=0.008, n=291). The cost of successfully rearing a litter to emergence was borne by the females that had given birth: the number of emergent pups from the previous litter was a significant negative correlate of conception for females that had given birth in the previous communal litter (χ^2=10.00, df=1, p=0.002, n=176) but was non-significant for females that had not given birth in the previous communal litter (χ^2=0.28, df=1, p=0.60, n=60) (Fig. 3). This result was consistent when a female's parturition status for the previous litter was replaced by her conception status for the previous litter.

Fig. 1 Body weight of female banded mongooses (*Mungos mungo*) (within the same cohort) that did and did not give birth, for breeding events where some but not all cohort members gave birth for the first time. Body weight measured within 32 days prior to conception (all females weighed on same day). Prediction from REML model with litter as the random model

Fig. 2a, b Effects on female age of first reproduction. *Solid lines* show predicted relationship (from GLM). *Dashed lines* indicate the standard error envelope. GLM accounted for 42.6% variation. **a** Effect of the mean number of reproductive females in the group (during the three oestrus events prior to the female reaching 230 days old) on age at first conception. *Diamonds* represent individual data-points, adjusted for rainfall. **b** Effect of mean daily rainfall (in the 150 days prior to the female reaching 230 days old) on age at first conception. *Diamonds* represent individual data-points, adjusted for number of reproductive females
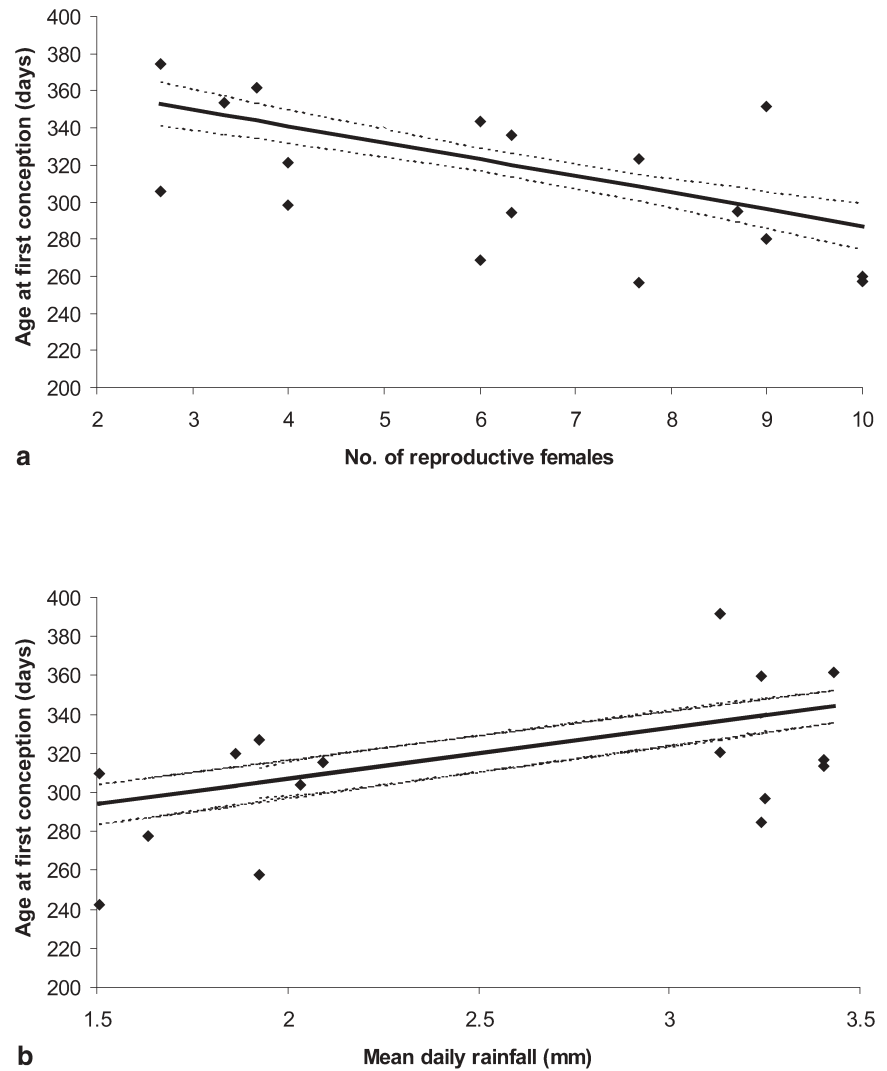
Inter-conception interval

The mean group inter-conception interval was 85.52±4.00 days (range 47–177). There was no evidence that inter-conception interval was affected by access to unrelated males or carer number. Inter-conception interval was shorter in larger groups, but increased in groups with more pregnant females (group size: $F_{1,47}=13.4$, $df=1$, $p=0.001$, $n=50$; number of pregnant females: $F_{1,46}=4.8$, $df=1$, $p=0.033$, $n=50$, Fig. 4). There was no evidence that inter-conception interval was affected by litter survival to emergence, access to refuse or rainfall.
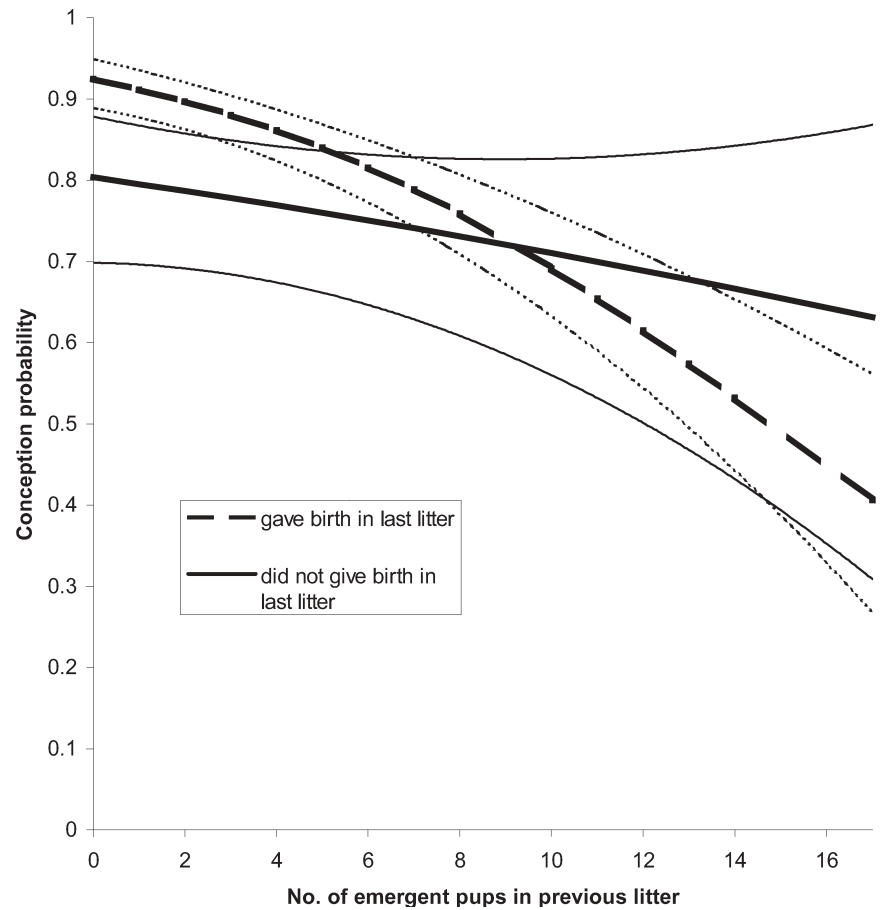
Foetus count

Foetus count was affected by individual factors but not affected by social and environmental factors. Average foetus count was 3.32±0.06 (range 1–6). Larger females carried more foetuses (head-width, $\chi^2=6.31$, $df=1$, $p=0.012$, $n=190$, Fig. 5; age: $\chi^2=5.10$, $df=1$, $p=0.024$, $n=196$). Neither pre-conception body weight nor body

condition were significant correlates of an individual's foetus count. Females that were mate-guarded did not carry more foetuses than non-mate-guarded females, and among females that were mate-guarded, there was no tendency for females of lower rank, or that were mate guarded later, to carry fewer foetuses. A female's foetal litter size was unaffected by access to unrelated males within the group, carer number, group size, the number of females in the group, rainfall, or access to refuse.

Foetus size

Larger females carried larger foetuses: foetus size was positively correlated with head-width (head-width: $\chi^2=7.56$, $df=1$, $p=0.006$, $n=154$; Fig. 6). After adjusting for head-width, females that had given birth in the previous litter had a non-significant tendency to carry smaller foetuses (parturition status for last litter: $\chi^2=3.33$, $df=1$, $p=0.068$, $n=78$). An individual's foetus size was not significantly correlated with age or pre-conception body weight. Foetus size was unaffected by whether or not a

Fig. 3 Effect of number of emergent pups in the previous litter on conception probability. *Bold lines* show predicted relationships (from IRREML with binomial distribution, denominator 1, and with litter as the random model). *Light lines* indicate the standard error envelopes

Discussion

This paper set out to evaluate the effects of individual, social, and environmental factors on fecundity in female banded mongooses. Whereas, in the majority of cooperative breeding species subordinates seldom breed, in the banded mongoose the majority of reproductive females conceive and most carry their litter to term. How do the factors affecting fecundity in species with high reproductive skew compare with those determining fecundity in the banded mongoose? The two major determinants of fecundity in species with high reproductive skew are dominance and access to unrelated males. Neither of these factors had a discernible effect on fecundity of female banded mongooses.

Do individual characteristics affect fecundity?

Whilst fecundity in female banded mongooses is consistently affected by intrinsic characteristics (especially age and body size), there is generally an absence of any effect of dominance. The lack of a distinct dominance hierarchy is likely to be an important factor in promoting low reproductive skew. If dominant females suppress reproduction in subordinate females, their control would be expected to be greater over younger, smaller females.

female was mate-guarded, her rank or when she was mate guarded relative to other females. There was no effect of foetus count on foetus size.

Abortion probability

A female's probability of abortion was affected by individual and social factors, but there was no effect of environmental factors. There were 18 suspected abortions (within six groups, distributed amongst 13 of 69 communal litters) and 246 successful gestations: an overall abortion rate of 6.8% (4.5% for parous females). The probability of abortion decreased with increasing age and body size (age: $\chi^2=8.15$, $df=1$, $p=0.004$, $n=256$, Fig. 7a; head width: $\chi^2=7.36$, $df=1$, $p=0.007$, $n=153$), with six females aborting during the gestation of their first litter. The probability of abortion was unaffected by body weight and body condition, and by whether or not a female was mate-guarded, her rank and oestrus order. Whilst a female's probability of abortion increased in groups with more carers (adjusted for age: $\chi^2=10.67$, $df=1$, $p=0.001$, $n=242$, Fig. 7b), it was unaffected by access to unrelated males within the group, group size, the number of females in the group, rainfall, and access to refuse.

Fig. 4a, b Effects on group inter-conception interval. *Solid lines* show predicted relationship (from GLM). *Dashed lines* indicate the standard error envelope. GLM accounted for 19.2% variation. **a** Effect of group size on group inter-conception interval. *Diamonds* represent individual data-points, adjusted for number of pregnant females.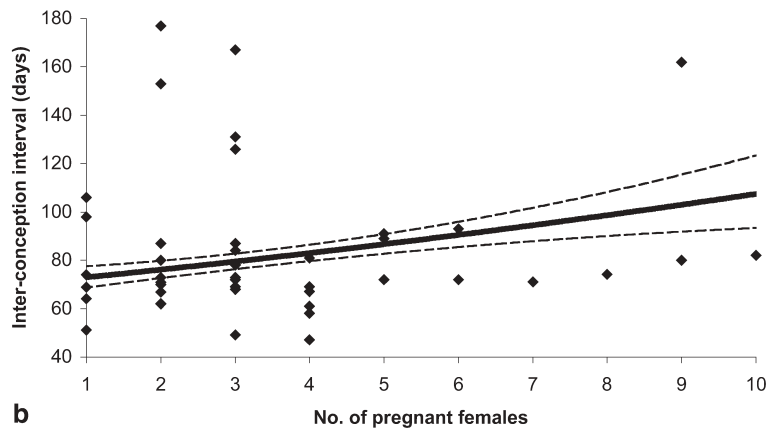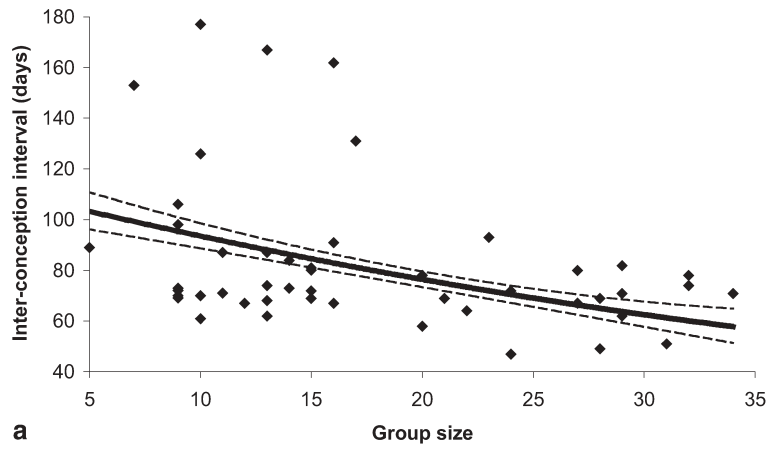 **b** Effect of number of pregnant females on group inter-conception interval. *Diamonds* represent individual data-points, adjusted for group size

Fig. 5 Effect of female body size (head-width in mm) on foetus count. *Solid line* indicates predicted relationship (from GLM with poisson distribution). *Dashed lines* indicate the standard error envelope. *Diamonds* represent individual data-points. GLM accounted for 15.4% variation
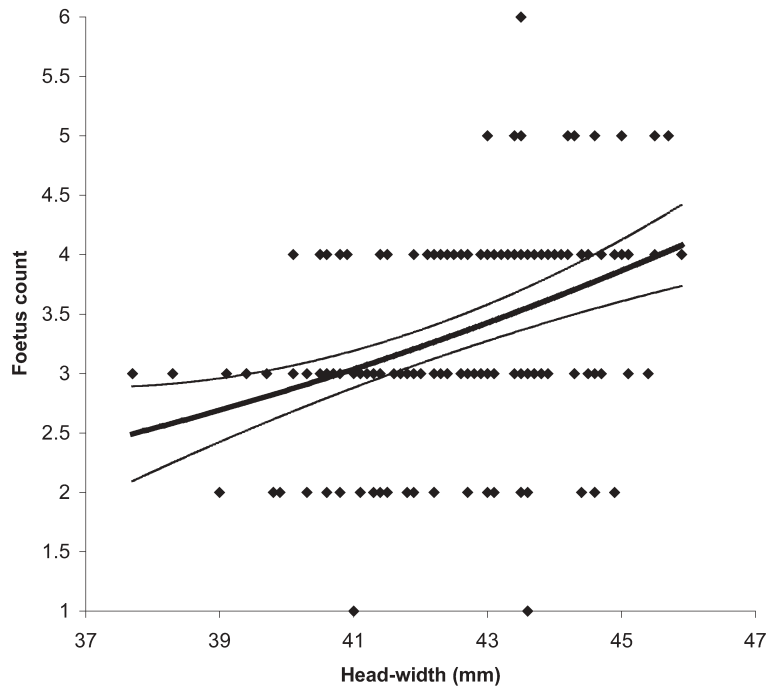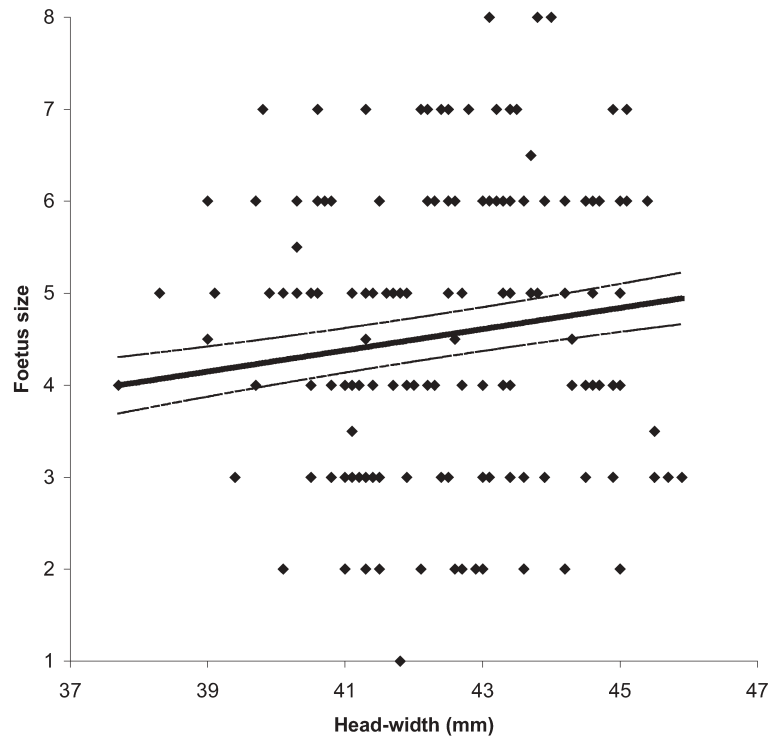
Fig. 6 Effect of female body size (head-width in mm) on foetus size (measured on a scale of 1 to 8). *Solid line* indicates predicted relationship (from REML, with litter as the random model). *Dashed lines* indicate the standard error envelope. *Diamonds* represent individual data-points

Models of reproductive skew (Johnstone 2000) therefore predict that young females would be less likely to conceive in groups with more reproductive females, or with low food availability. However, this was not the case in this study. There is no suggestion of social control of reproduction in the banded mongoose. That fecundity is unaffected by dominance (also see De Luca and Ginsberg 2001) suggests either that 'dominant' females lack the ability to control subordinate reproduction, or that there is no benefit to 'dominant' females in suppressing subordinate reproduction.

Egalitarianism is likely to occur where one female is unable to control the reproduction of another (Clutton-Brock 1998; Reeve et al. 1998). In contrast to females in species with well-developed dominance hierarchies, where regular harassment and dominance displays occur (e.g. Malcolm and Marten 1982; Reeve and Sherman 1991; Creel et al. 1992; Clutton-Brock et al. 2001b), female banded mongooses do not display dominance behaviour during everyday social interactions, or even during oestrus (J.S. Gilchrist; unpublished data). Competition for food is sporadic, dyadic, and the owner almost always wins. In these respects, female banded mongooses are similar to female lions, that also exhibit low reproductive skew (see Packer et al. 2001). Creel and Waser (1997) suggest that a dominance hierarchy is a precondition for 'suppression' because ritualised displays of dominance, as seen in many carnivores, are hypothesised to have evolved as honest displays of fighting ability and therefore leverage (Grafen 1990). It could, however, be argued that the lack of an obvious dominance hierarchy in species with low reproductive skew is a consequence of

low skew, rather than a prerequisite (Keller and Reeve 1994; see also Jamieson 1997).

An alternative possibility to females lacking the ability to control other's reproduction is simply that there is no benefit to a female in suppressing another's reproduction. Cant (2000) suggested that there is no cost to a banded mongoose female's reproductive success when breeding in the presence of other females, and therefore no incentive for reproductive suppression. In the lion, females actually benefit by breeding in the presence of additional females, through increased cub survival in crèches (Packer et al. 2001). Similar beneficial effects to communal breeding may occur in banded mongooses (see Cant 2000). Communal breeding may therefore be adaptive, rather than simply a failure to evolve mechanisms for an individual to promote its' personal lifetime reproductive success.

The absence of apparent dominance effects on fecundity is not to say that elements of a female's physical characteristics do not affect fecundity. Individual characteristics were the most consistent correlates of fecundity, with body size or age usually the strongest predictor. However, within reproductive females, conception probability did not differ with age or body size. This contrasts with the dwarf mongoose and meerkat, where normally only the socially dominant female (generally the oldest or largest) breeds, and subordinates that breed are older and larger (Creel and Waser 1991; Clutton-Brock et al. 2001a). That young females were more likely to abort may be due to their inexperience, physical immaturity or susceptibility to stress (Wasser and Barash 1983; although see Packer et al. 1995).

Fig. 7a, b Effects on abortion probability. *Solid lines* show predicted relationship (from GLM fitted with binomial distribution, denominator 1). *Dashed lines* indicate the standard error envelope. **a** Effect of age on abortion probability. **b** Effect of number of carers on abortion probability
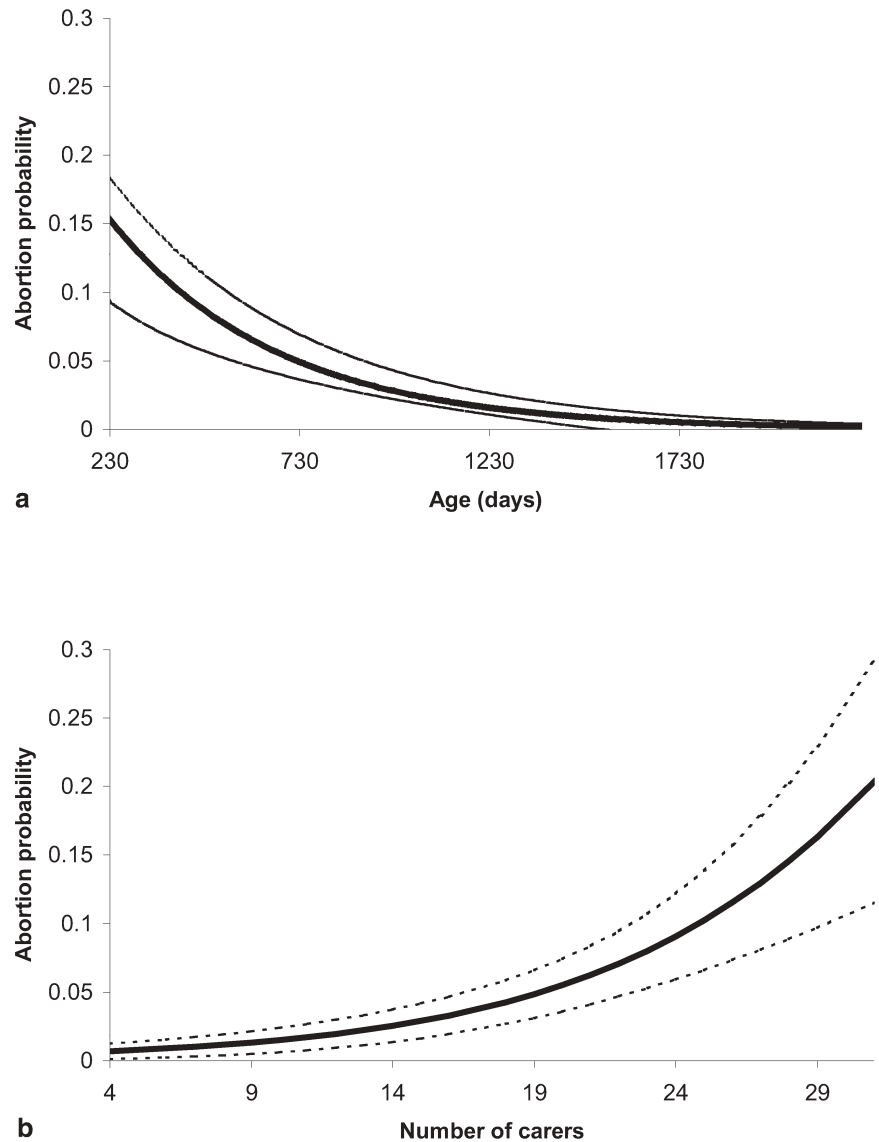
It has been shown that whilst female banded mongooses exhibit a clear hierarchy in mating order within their group, females generally give birth synchronously (Cant 2000). Therefore, late mating females (which are generally younger) have a shorter gestation period (Cant 2000). This raises the intriguing possibility that younger females may carry fewer foetuses to compensate for a reduced gestation period. Whilst foetus count increased with age in our study, there was no correlation between foetus count and the order in which females were mate-guarded during oestrus. The age effect on foetus count is therefore independent of mating order (and gestation period), and the number of foetuses gestated is probably restricted by physical size. Berger (1992) showed that female mammals are capable of reducing gestation period to synchronise parturition by producing smaller neonates, but we found no evidence that female banded mongooses that mated later gestated smaller foetuses, or that females that carried smaller litters gestated larger foetuses.

Is there evidence of inbreeding avoidance?

One of the principal factors for low reproductive skew in the banded mongoose is the apparent lack of an inbreeding barrier. Access to unrelated males within the group had no effect on any measure of fecundity, and all females mated and conceived their first litter within their natal group. There was therefore no evidence of inbreeding avoidance, or of inbreeding depression prior to parturition.

There are three possible explanations for the apparent absence of inbreeding avoidance: (1) inbreeding depression has been alleviated through the purging of deleterious alleles in a highly inbred population (Kirkpatrick and Jarne 2000); (2) the costs of avoiding inbreeding exceed the costs of inbreeding (Waser et al. 1986; Keane et al. 1996; McRae 1996); or (3) females regularly mate with extra-group males (see Cant et al. 2002 regarding banded mongooses). There appears to be no incest taboo in this population of banded mongooses; females regularly mate

with potential fathers, brothers and sons, and the incidence of apparent incestuous matings is much greater than that of inter-group matings (J.S. Gilchrist, unpublished data). Genetic analysis confirms that the Mweya banded mongoose population is inbred, and that individuals regularly breed with close relatives within their group (R.C. Waldick, J.S. Gilchrist, S. Hodge, B. Amos, unpublished work). In this respect, the banded mongoose is similar to the dwarf mongoose, which shows no evidence of inbreeding avoidance or depression in a population with a history of inbreeding (Keane et al. 1996). However, in the banded mongoose, individuals in mixed sex eviction events consequently split into two single sex subgroups to disperse (Cant et al. 2001; J.S. Gilchrist, unpublished data), suggesting that out-breeding is beneficial under certain circumstances.

Do social factors affect fecundity?

Whilst fecundity often decreases with increasing density, group size, or the number of reproductive females in non-cooperative breeding social animals (e.g. Clutton-Brock et al. 1983; Hoogland 1995; Ostfeld and Canham 1995), in many high skew cooperative breeding species reproductive success increases with group size due to the effects of helpers (Emlen 1991; Jennions and Macdonald 1994; Cockburn 1998). How does group size affect fecundity in the low skew banded mongoose? There was no effect of group size on a female's age at first reproduction, but females conceived their first litter at a younger age in groups with more reproductive females. This suggests that neither resource nor sexual competition delay a female's reproductive maturation. Group inter-conception interval decreased with increasing group size, but increased with increasing number of breeding females. This indicates that, whilst increasing group size is advantageous to breeding frequency, there are specific costs to increasing numbers of reproductive females. Similarly, inter-birth interval increases with the number of breeding females in the majority of primate species (van Schaik 1983), and this has been directly attributed to female-female competition (citations in Hill et al. 2000). However, such effects are rarely considered in studies of reproductive skew, where negative effects of subordinate breeding on dominant fitness are evaluated for the current brood or litter, but effects on future reproductive success are generally overlooked.

Although carers improve breeding success post-parturition in banded mongooses (Gilchrist 2001, 2004), there is no evidence that they affect female fecundity. Neither the number of carers, nor group size explained independent variation in age of first conception, probability of conception, or foetus count. That abortion was more frequent in groups with more carers, likely reflects a cost of increasing group size. Therefore, as for meerkats, there is no evidence that a female increases litter size when there is more help available (Russell et al. 2003).

Do environmental factors affect fecundity?

The relatively high rainfall, and consequent high availability of the banded mongooses invertebrate prey, is likely a prerequisite for low reproductive skew. Whilst rainfall determines when conditions are suitable for reproduction (Rood 1975; Cant 1998; Gilchrist 2001), it does not differentially affect the ability of females to conceive within a group: when breeding occurs, the majority of females are in good enough body condition to conceive and carry to term. Similarly, females in groups with access to refuse (a source of supplementary food: Gilchrist and Otali 2002; Otali and Gilchrist 2004) were no more fecund than those in groups with access to only natural food. This result contradicts that of Otali and Gilchrist (2004) who, using a simpler analysis that did not account for other factors, showed that females in refuse-feeding groups gestate slightly larger litters. The lack of a refuse-feeding effect is surprising because females may be expected to increase their investment when resources are more abundant, as in food supplemented populations of other species where females increase litter or brood size (see citations in Otali and Gilchrist 2004).

Conclusions

Reproductive suppression of subordinates in social groups can be promoted by a number of factors: strong environmental constraints; lack of access to unrelated partners; or benefits to the dominant of subordinate suppression, combined with high dominant leverage. The relative rarity of cooperative breeding species with low reproductive skew (Creel and Waser 1997) may be because low skew requires relaxation of all these selection pressures, whereas any one of the above promote high skew breeding systems. Female banded mongooses in the population studied may be unusual in having a combination of factors that result in low reproductive skew. Food availability is relatively high, there is no inbreeding barrier, and there is no distinct dominance hierarchy. Similarly, females of the only other communally breeding carnivore with low reproductive skew, the lion, experience high food availability, access to unrelated males, low dominant leverage, and benefits to communal crèches (Packer et al. 2001). It is also interesting to consider that within social groups of both banded mongooses and lions (and numerous communal breeding rodents; Hayes 2000) females are related. When resources exceed the requirements of a single 'dominant' female, for whom an increase in litter size would be prohibitively costly, such a female may gain indirect fitness benefits by allowing related females to produce young (assuming that those young are not costly to the fitness of the 'dominant' female's offspring; Cant and Johnstone 1999).

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