

Factors predicting the frequency, likelihood and duration of allonursing in the cooperatively breeding meerkat

K.J. MacLeod^a *, J.F. Nielsen^{b, c}, T.H. Clutton-Brock^{a, d}

^a Large Animal Research Group, University of Cambridge, Cambridge, U.K.

^b Institute of Evolutionary Biology, University of Edinburgh, Edinburgh, U.K.

^c Institute of Zoology, Zoological Society of London, London, U.K.

^d Mammal Research Institute, University of Pretoria, Pretoria, Republic of South Africa

* Correspondence: K. J. MacLeod, Department of Zoology, Downing Street, Cambridge CB2 3EJ, U.K. E-mail address: kjm54@cam.ac.uk (K. J. MacLeod).

Allolactation, the nursing of another female's offspring, occurs most commonly where several females raise young simultaneously in the same nest, but also occurs in singular breeders where non-breeders also lactate for the offspring of dominant females. In this study, we investigate the factors predicting the frequency of allonursing, whether or not subordinate female meerkats invest in allonursing, and how much time they invest. Around half of all litters born to dominant females were allonursed. Litters born later were more likely to be allonursed than those born early in the season. Group size, litter size, rainfall, and maternal condition were not associated with the likelihood that a litter was allonursed. Subordinate females were more likely to allolactate if they were (or had recently been) pregnant. This effect was stronger if they were also highly related to the litter's mother, suggesting that females may gain indirect benefits from allolactating. Older females and those that had recently returned to the group following eviction were also more likely to allolactate.

Females nursed for longer periods if they were in good condition, and invested more time if the litter was large or if the litter mother was in poor condition. We suggest that allolactation generates a combination of direct and indirect benefits.

Key words: allolactation, helper, meerkat, *Suricata suricatta*

INTRODUCTION

Alloparental care of offspring is care provided by any individual other than the genetic parents (Wilson 1975). Care of non-descendent young is common in birds (Cockburn 1998), fish (Wisenden 1999), mammals (Riedman 1982), and the social insects (Wilson 1971), and encompasses a suite of behaviours including defence; guarding; feeding; and, in mammals, carrying and nursing of young (Riedman 1982; Lewis & Pusey 1997). Although the extent and manifestation of alloparental care differs between species, it is hypothesised that it is maintained across taxa by providing alloparents with similar adaptive benefits: helping to rear kin may provide indirect fitness benefits; reciprocation may be expected; helping may facilitate continued access to group benefits; or may provide valuable parenting practice (Riedman 1982).

Allolactation, or allonursing, is the nursing of another female's offspring, usually, but not exclusively, when females are also nursing young of their own (Packer et al. 1992; Roulin 2002). This form of alloparental care occurs across a wide variety of mammals, most commonly where multiple females breed at the same time, and nest communally (Packer et al. 1992; Roulin 2002). The benefits for offspring of being nursed by more than one female are likely to be substantial, both in terms of survival and growth, and the transfer of immune compounds (Roulin & Heeb 1999; König 2006). Although lactation is costly for lactators

(Clutton-Brock et al. 1989), where females breed communally allolactators may face little net cost except a possible increase in disease transmission (Roulin & Heeb 1999). As all mothers produce milk and, as there is a high chance that the allolactator's own offspring will receive milk from another mother, discriminating against non-offspring may provide limited benefits (Lewis & Pusey 1997), and in fact, may even be selected against (Roulin & Hager 2003).

Less commonly, allonursing occurs in singular breeders where only one female produces offspring and allolactators do not have litters of their own (Creel et al. 1991). There are a number of potential explanations for allolactation in singular breeders. Allolactation may, for example, provide allolactators with indirect benefits in closely-related groups; communal nursing is more common in species which nest with kin (Hayes 2000), and females often preferentially nurse related offspring over less or non-related young (Rood 1980; McCracken 1984; Pusey & Packer 1994). Additionally, investing in non-offspring may provide fitness benefits to allolactators through group augmentation (Kokko et al. 2001). A number of studies have shown that individual fitness increases with group size, either directly (Packer & Ruttan 1988; Roberts 1996), or through delayed benefits (Wiley & Rabenold 1984).

To understand why females nurse non-offspring, it is important to understand the circumstances in which it occurs. Although allonursing has been observed in many species (Packer et al. 1992), few descriptive studies exist that allow investigation of the potential factors that predict the likelihood of allolactation in a single study system. Furthermore, few studies have been able to investigate the extent and duration of allosuckling in singular breeders, where allolactators do not have litters of their own. This study investigates the potential links between individual, group and environmental characteristics on the probability of allolactation in a singular cooperative breeder, the Kalahari meerkat (*Suricata suricatta*), using a long-term database. Allolactation occurs regularly in meerkats, which live in groups

of up to 50 animals of equal sex ratio (Clutton-Brock et al. 1999a). Breeding opportunities are monopolised by a single behaviourally dominant female, who maintains her position through aggressive suppression of subordinate breeding attempts through eviction or infanticide (Clutton-Brock et al. 1998). Though subordinate individuals may occasionally breed, non-breeding helpers of both sexes help to rear the offspring of the dominant female by babysitting and provisioning pups (Doolan & MacDonald 1997; Clutton-Brock et al. 1999b; Clutton-Brock et al. 2001a). As well as feeding and babysitting pups, subordinate females also allonurse pups born to dominant females (Clutton-Brock et al. 1999b; Doolan & McDonald 1999). Females suffer substantial weight loss as a result of allolactation (Scantlebury et al. 2002).

To determine why subordinate female meerkats allonurse pups born to the dominant female when they do not have litters of their own, our analysis focuses on four main questions. First, what is the frequency of allolactation in wild meerkat groups? Allolactation has been recorded in our study population (Doolan & Macdonald 1999, Clutton-Brock et al. 1999b), but the frequency of its occurrence, how many females participate, and for how long, has not been determined. Second, what factors predict the likelihood that a litter born to a dominant female will be allonursed? Litter and maternal characteristics related to the demands of the litter are also likely to influence the probability of allonursing. For example, meerkat females adjust their contributions to other alloparental behaviours according to litter size: female helpers provision larger litters with more food items than smaller litters (Clutton-Brock et al. 2001a). Rainfall governs the short-term availability of food, and therefore, helper condition (English et al. 2012); resultantly, rainfall is also likely to be linked to whether a litter is allonursed. Third, what factors predict the likelihood that individual subordinate females will allolactate? Allolactation likelihood is most likely linked to whether or not a female is or has recently been pregnant, though spontaneous lactation has been shown in the

dwarf mongoose (Creel et al. 1991), and has also been reported in the meerkat (Doolan & MacDonald 1999). Relatedness to the litter mother and the likelihood of gaining indirect benefits may predict whether a female allolactates, as in other species which allonurse selectively (McCracken 1984; Pusey & Packer 1994). The likelihood of allolactating may be condition-dependent. Other alloparental behaviours are dependent on body condition – for example, experimentally-fed helpers provision pups more (Clutton-Brock et al. 2001a). Other factors, such as age, and whether a female has been recently evicted may also correlate with the probability of her allolactating. And fourth, if a subordinate female allolactates, what predicts her level of investment in this behaviour? Parameters likely to predict levels of contribution to allolactation include a combination of individual and litter characteristics: body condition of both the allolactator and mother, litter size, relatedness to litter mother, and the number of co-allolactators. We predict that large litters born to mothers in poor condition are more likely to be nursed for longer, and that allolactators in poor condition, or those nursing litters with higher numbers of co-allolactators, will nurse for shorter periods. As the majority of pup nursing occurs below ground, we are unable to determine factors influencing whether or not individual pups were allonursed, or whether they seek allonurses.

METHODS

Data collection and study site

All data were collected at the Kuruman River Reserve in the Kalahari region of South Africa (26°58' S, 21°49' E) between December 1996 and April 2011. Details of climate and habitat are described elsewhere (Russell et al. 2002). The study population observed over this period includes over 40 social groups. All individuals were habituated to close human proximity (<1 m), and could be identified by unique dye-mark patterns which were applied

and maintained while the animal rested without the need for capture (Hodge et al. 2008). All meerkat groups were visited every 1-3 days, and the majority of individuals (>95%) were able to be weighed on electronic scales (± 1 g) using small crumbs of hard-boiled egg as enticement (Clutton-Brock et al. 2004); consequently, pregnancies were easily detectable in their later stages, and birth dates could be identified to within 3 days, due to substantial changes in weight and appearance. Female dominance status could also be readily identified, as the dominant female is the primary breeder in the group whilst all subordinate females are behaviourally submissive to her (O'Riain et al. 2000; Clutton-Brock et al. 2001b).

Frequency of allolactation

Using the long-term database, the birthdates of all litters carried to term and associated lactation periods were identified. Lactation was easily detectable due to obvious suckle marks around the nipples after emergence from the burrow in the morning, which persist until the female stops lactating. The date on which females first display suckle marks was recorded as the start of lactation, and the first date on which the female shows no sign of lactation (no dampness around the nipple, no attached sand, and pups do not attempt to suckle when near the burrow) was recorded as the end of lactation.

Litters born to dominant females were given a binary code identifying whether they were nursed by more than one female ("1"), or only by their mother ("0"). Litters which had been nursed by one or more female(s) in addition to their mother ("1") were defined as having been allonursed.

All possible allolactators were identified for each litter. Potential allolactators were defined as all adult females (females older than 6 months of age) present in the group, on the

litter's birthdate, that was not the litter mother. Whether or not each potential allolactator had a recorded lactation period associated with the litter in question was again recorded as a binary response ("0" – no, "1" – yes).

Factors affecting the likelihood that a litter is allonursed

The following data were extracted for each litter: litter size at emergence; total rainfall (mm) in the month before litter birth; the order in which that litter was born within the group during that season; group size; and maternal mass and age.

Litter order within season was determined as follows: the first litter was the first born to any female in or after July of which at least one pup survived to weaning; any litters born in the group after this are ordered accordingly. July was deemed the first month of the season as, though meerkats breed all year round, the biggest drop in births is May-July, after which litter births are, at least across the population, fairly constant, reaching a peak in Nov-Dec. We used litter order, not month, because meerkat groups may produce the first litter of the year anytime between August and February (K MacLeod, unpublished data), therefore, litter order contains more information than regarding the presence of pups in the group, as well as the relative earliness or lateness of the litter specific to the group it is born into. Rainfall in the 30 days prior to an event is an established proxy for resource availability during that time in this system (Hodge et al. 2009), and accounts for effects of environmental variation. Group size is the total number of adults (individuals over 6 months) in the group at the time of litter birth. Meerkat litters are born in an underground burrow from which they emerge when they are approximately three weeks old (Russell et al. 2002). Few pups are lost during the birth-emergence period, unless the whole litter is lost or killed; this has been confirmed by ultrasonic imaging data (Russell et al. 2003). Litter size at emergence was therefore

judged to be a suitable proxy for the same measurement at birth. Of the 316 litters in this dataset, full litter characteristic data were available for 225 litters born to dominant females. Mean maternal age is 1696 ± 632.07 days, and mean maternal mass is 772.5 ± 70.57 g.

As female pregnancy weight is influenced by the number of foetuses, we used maternal mass at conception as a more representative measure of body condition. Mass at conception was calculated as the mean of all morning pre-foraging mass records in the week after the conception date. In a small number of cases the gestation period is shorter than the average of 70 days (Sharp et al. 2012); because interbirth intervals are also commonly short, using weights from the week after conception (during which there is no discernible pregnancy-related weight gain) instead of the week before reduced the risk of including weights recorded while the female was still pregnant with a previous litter. Age was measured in days from the date of birth to the date of conception.

Assessment for colinearity between variables showed that female mass and age were strongly positively correlated ($r=0.77$, $P<0.001$). We therefore replaced mass in all models with the residuals of a biphasic growth model to provide an alternative measure of body condition – whether a female was heavy or light for her age, according to the predictions of the model (English et al. 2012). This removed the correlation with age.

Factors affecting the likelihood of a female to allolactate

For each litter, the following information on all potential allolactators present was extracted: weight, age, relatedness to the litter mother, and pregnancy and eviction status. Female mass was calculated as the mean of all morning pre-foraging mass records in the week before the

litter birthdate. Age was measured in days from the date of birth of each female to the litter birthdate.

All females used in this study form part of The Kalahari Meerkat Project population which has been intensively monitored and sampled for tissue since 1993, and for which a genetically-validated pedigree has been constructed (Nielsen et al. 2012). For DNA analysis, a 2- to 5-mm tissue sample from the tail tip of each pup is taken at emergence, a procedure which has no adverse effects on pups (Spong et al. 2008). Tissue samples from recently habituated or immigrant adults were taken from anaesthetized or dead animals (Nielsen et al. 2012). DNA was extracted from tissue samples and genotyped at up to 18 variable microsatellite loci, and familial relationships were then inferred by using a combination of behavioural records, microsatellite data, and two programs: MasterBayes v.2.47 (Hadfield et al. 2006) and COLONY 2 v.2.0.1.1 (Wang 2004). Candidate fathers were defined as any male alive in any group during the two-week window surrounding conception (i.e. 63-77 days prior to pup birth), whereas most maternities could be accurately determined from pregnancy records. Where maternity was uncertain (i.e. when more than one female gave birth in the same burrow), all the females known to have given birth in the group at the time of pup birth were considered as candidate mothers. The roving frequency of males, the gestational status of females, and the sex, dominance status and group membership of all individuals were provided as phenotypic descriptors in MASTER BAYES. Only genetic parentage assignments with at least 80% individual-level confidence (average parentage assignment confidence = 95.57%) were considered when combining the inferences from both programs, which resulted in a seven-generation deep categorical pedigree for the entire population. Founders and immigrants to the population were assumed to be unrelated. The percentage of genes shared by common descent between each pair of individuals in the population, or the coefficients of relatedness (R), were calculated from links in the pedigree

using PEDANTICS (Morrissey and Wilson 2010). Due to the depth in the pedigree and the ability to detect accumulated inbreeding events, R-values ranged from 0 to 0.66, (where parent-offspring R was inflated by a history of repeated inbreeding events). From this data, relatedness coefficients could be calculated for each female dyad (litter mother, potential allolactator).

On the birthdate of each litter, the pregnancy and eviction statuses of each adult female in the group, excluding the mother, were recorded. The status of these potential allolactators fell into the following categories: pregnant (“Y”), not pregnant (“N”), or recently having given birth, aborted, or lost a litter (“R”). The average meerkat gestation period is 70 days (Russell et al. 2002). Pregnancies can be detected around one month after conception; therefore, pregnancies which are terminated at less than one month cannot be detected. If a female was first recorded as being pregnant less than one month after a litter birthdate, or gave birth less than 70 days after a litter birthdate, she was recorded as pregnant at the time of that litter’s birth. If a female had given birth, aborted, or lost a litter less than one month before the birthdate of a litter, she was coded as “R” (recent birth/ loss) at the time of that litter’s birth. Infrequently (<10 instances of 65 “recent” pregnancies), a subordinate female carried her own litter to term, and nursed it while also apparently nursing a litter born to the dominant female. Here allonursing may represent milk-stealing and not active alloparental care. It is also difficult to determine conclusively whether there is milk transfer to the dominant pups. We therefore excluded these females and litters from the following analyses.

The eviction statuses of all potential allolactators within a group were determined on a case by case basis. Females were coded as having either been evicted within the month prior to a litter’s birthdate, or not.

Data on 316 litters born to dominant females were extracted, with a total of 1348 present females distributed among these. Whether a female present in a group at the time of a litter's birth allolactated or not was fitted as a binary response variable in a series of generalized linear mixed models to investigate potential correlations with female condition (age and mass), relatedness to the litter mother, and pregnancy and eviction status. Female identity and litter were included as random terms to prevent problems of pseudoreplication due to non-independence of multiple samples of the same female, and of different females present in groups on the birthdate of the same litter.

Factors affecting how long subordinate females allonursed

The time in days between the recorded onset and cessation of allolactation was calculated for each female that allolactated – this is the allolactation period. Where an end date coincided with the death of the litter the female was allonursing, the allolactation period was recorded as being artificially shortened, and was not included in analyses of factors affecting allolactation duration. Likewise, records without sufficient accuracy (either the start or end of lactation had occurred when the female had not been seen for over 7 days) were excluded from analyses. Resultantly all records of duration lengths used in analyses were accurate to within a week.

To determine whether subordinate female time investment in allolactation is predicted by the condition of the allolactators or litter size, the following data were extracted for each female allolactation period where data on duration was available ($N=121$): litter size, and the age and weight of the litter mother at conception, the total number of females which had allolactation periods associated with the litter in question, and the age and weight of the lactator at the beginning of her allolactation period. In each case, as before, we used the

residuals of biphasic growth models (English et al. 2012) to replace mass and age in all models.

Statistical analyses

A global model was defined for each dataset using the lme4 package (Bates et al. 2008), both with a logit link function and a binomial error distribution. The explanatory variables and all potential biologically significant interactions in each model produced a set of candidate models which were then compared using the AIC_c (the second order Akaike Information Criterion), with the lowest AIC_c value indicating the best model fit (Akaike 1974). A subset of models was generated by calculating the difference between the AIC_c value of the best-fitting model and all other models, and using a cut-off of 2 AIC_c as criteria for inclusion in the subset. This subset of models was then averaged using the MuMIN package (Bartón 2009), combining the parameter estimates of all models relative to their weight (Burnham & Anderson 2002, and following Grueber et al. 2011). All means are reported with standard deviations.

RESULTS

Frequency of allolactation

Allolactation occurred in 152 (48.1%) litters out of a total of 316 litters born to dominant females. Almost half (73 litters) were allonursed by only one female in addition to their mother. The maximum number of allolactators per litter was 7 (which occurred in only one litter) and the mean number per litter was 1.83 ± 1.08 . Where allolactation did occur, $31.9 \pm$

17.8% of the adult females present allonursed the litter ($N=152$). Each litter was allonursed for around 30 days (mean = 30.45 ± 14.47), and its duration varied from 2 to 68 days with a median value of 29.5. Allonurses provide milk for shorter periods than litter mothers, which lactate for around 50 days for their own pups (mean = 51.79 ± 9.25 days, $N=275$).

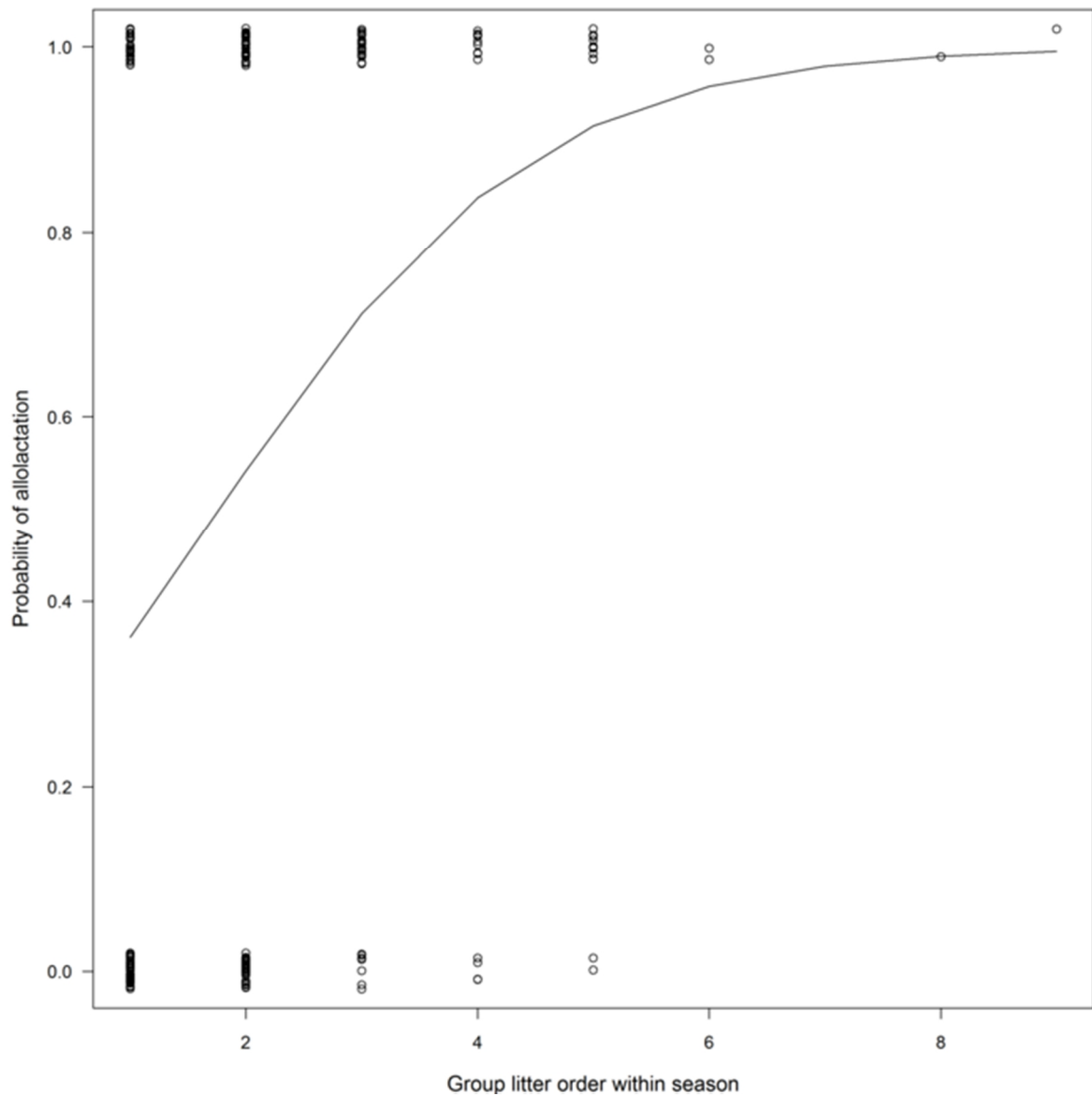


Fig. 1. The proportion of females which allolactate increases with the litter order within a breeding season: later litters are more likely to be allonursed ($p < 0.001$).

Factors affecting the likelihood that a litter is allonursed

Litters born later in the season relative to other litters born within the same group were significantly more likely to be allonursed (Fig. 1): the order in which a litter was born within the group during the breeding season was the most important factor predicting whether the litter received alloparental care in the form of allolactation, according to model-averaging (Table 1; see also Appendix 1 for top model set). This was the only variable which appeared in the best model. Group size, rainfall and residual maternal weight did not appear to explain any variation in allolactation likelihood according to model averaging – they appeared in one of the four top models each, and each ranked relatively low in relative variable importance. Litter size also does not predict the likelihood that a litter is allonursed – it appeared in none of the top models.

Table 1. Model averaged coefficients of generalized linear mixed models of factors potentially affecting the likelihood of a dominant litter receiving alloparental care in the form of allolactation, and the results of the best model. Litter size appeared in none of the top models.

Fixed effect	Estimate	SE	Relative variable importance	
intercept	-1.396	0.393		
Litter order	0.821	0.162	1.00	
Rainfall	-0.088	0.130	0.27	
Maternal weight relative to age	0.001	0.002	0.19	
Group size	0.008	0.025	0.17	
Best model	Estimate	SE	z value	p value
intercept	-1.37	0.36	-3.82	<0.001
Litter order	0.81	0.16	5.13	<0.001

Factors affecting the likelihood of female allolactation

More subordinate females allolactated if they were pregnant at the time or had given birth or lost a litter in the previous month than females that were not pregnant, according to model averaging (Table 2; Fig. 2d). Female body mass did not correlate with allolactation likelihood, but older subordinate females were more likely to allolactate than younger subordinates (Fig.2 a-b). Subordinate females also had a higher probability of allolactating if they had been temporarily forced out of the group by the dominant female (an “eviction”) in the previous month.

Table 2. The results of a generalized linear mixed model of factors affecting a subordinate female’s likelihood of allolactating.

Best model		Estimate	SE	z value	p value
intercept		-24.56	2.57	-9.54	<0.001
Pregnancy status	Not pregnant	0.00			<0.001
	Pregnant	2.45	2.56	0.96	
	Recently pregnant	11.86	2.98	3.98	
Age		8.02	1.82	4.408	<0.001
Eviction status	Not evicted	0.00			<0.05
	Evicted	2.37	2.0	1.19	
Relatedness		0.99	1.54	0.64	0.52
Mass		-0.26	1.10	-0.24	0.81
Pregnancy	Not Pregnant	0.00			<0.001
status*Relatedness	Pregnant	3.02	3.09	0.98	
	Recently pregnant	4.44	2.35	1.89	

Submodels were derived from a global model using a cut off of $2AIC_c$ greater than the best fitting model. There was only one model in this subset as all other had an $AIC_c > 2$; this is the best model. Female (n=519) and litter identity (n=524) were included as a random term in each model.

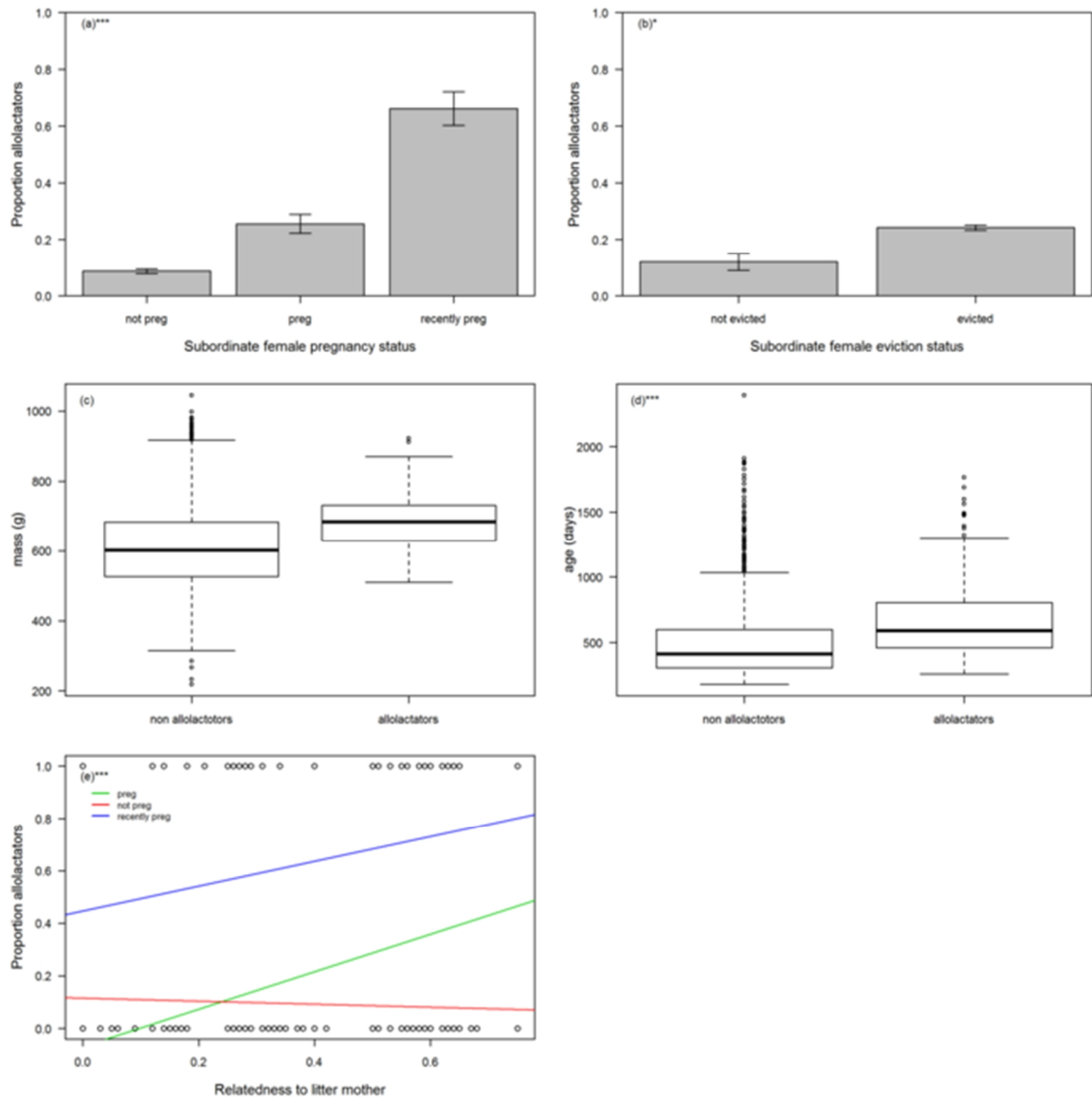


Fig.2. Factors affecting subordinate female allolactation likelihood: a) pregnancy status; b) eviction status in month before litter birth; c) body mass (note that actual mass (g) is used here for interpretive purposes, but residual mass from the meerkat growth curve was used in the model); d) age; e) interaction between relatedness and pregnancy status. Significance (in best model) denoted as follow: * = <0.05; ** = <0.01; *** = <0.001. Mass did not have a significant effect on allolactation likelihood. Boxplots display medians and interquartile ranges. Barplots display standard error.

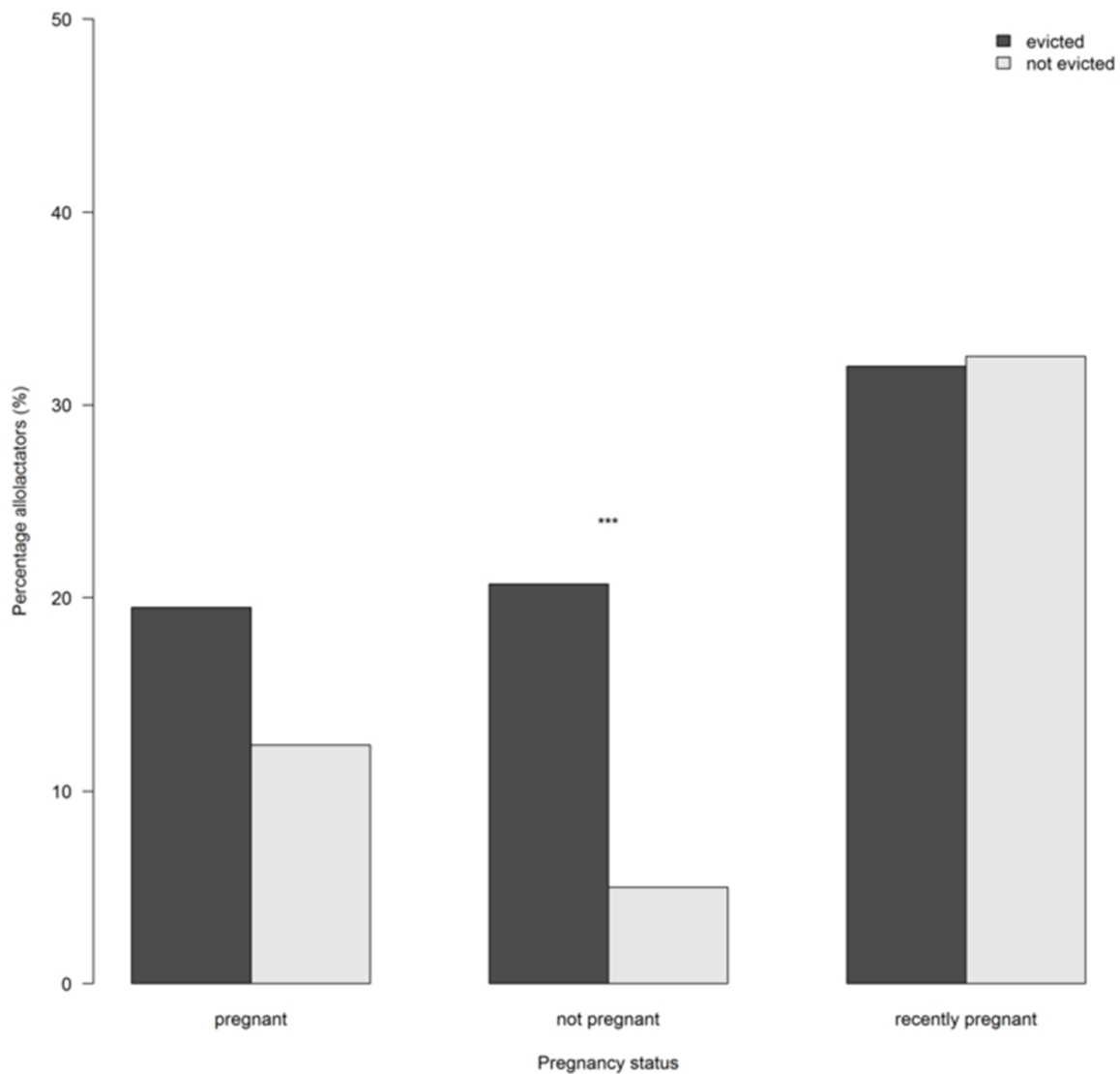


Fig. 3. The percentage of females which allolactated in each pregnancy status category (see Methods), according to whether they were recently evicted, or not. (***) denotes the only significant difference between evicted and non-evicted females - in the not pregnant category (Mann Whitney test: $W=172033$, $p<0.001$).

Previous studies have found a link between eviction and the likelihood of subordinate abortion (Young et al. 2006), but in this study less than 10% of recently pregnant females had been evicted (25 out of 262 recently pregnant females), and the probability of recently pregnant females allolactating is high whether or not they have been evicted. The positive

correlation between recent pregnancy and allolactation is therefore unlikely to be affected by eviction status. In contrast, eviction status predicts the likelihood that pregnant and non-pregnant females will allolactate: non-pregnant females which had recently been evicted were more likely to allolactate than non-pregnant females which had not been evicted in the past month (Mann Whitney test: $W=172033$, non-evicted, not preg $N=975$; evicted, not preg $N=139$; $P<0.001$; Fig.3.).

Relatedness predicts the probability that pregnant and recently pregnant females will allolactate but not the allolactation likelihood of a non-pregnant female (Table 2). Relatedness to the litter mother interacted with pregnancy status in a positive correlation with allolactation probability (Fig. 2d.). Of all the possible models (see Methods), none were within 2 AICc of the global model and the global model is therefore the best model.

Table 3. Model averaged coefficients of generalized linear mixed models of factors potentially affecting the duration of allolactation for dominant litters, and the results of the best model.

Fixed effect	Estimate	SE	Relative variable importance	
intercept	23.01	5.29		
lactator weight relative to age	0.07	0.02	1.00	
maternal weight relative to age	-0.05	0.02	1.00	
litter size	2.12	1.03	0.78	
number of allolactators	-0.7	0.92	0.23	
Best model	Estimate	SE	t value	p value
intercept	20.99	4.5	4.67	
lactator weight relative to age	0.07	0.02	4.40	<0.0001***
maternal weight relative to age	-0.05	0.02	-2.65	<0.01***
litter size	2.02	1.02	1.98	0.05*

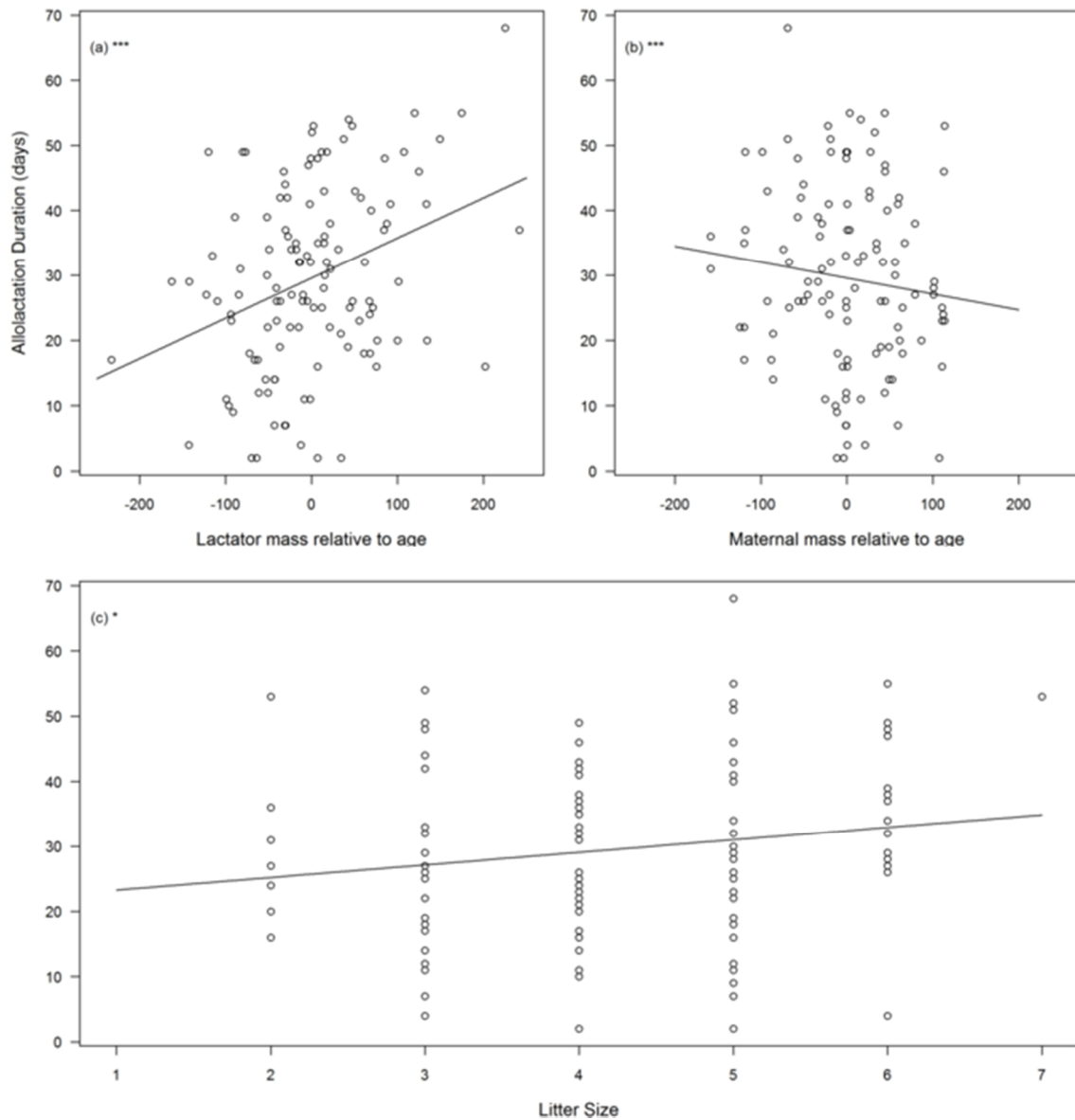


Fig.4. Factors affecting subordinate female investment in allolactation, in terms of how long she allonursed (days): a) lactator mass relative to her age, b) maternal mass relative to age, and c) litter size. Significance (in best model) denoted as follow: * = <0.05; ** = <0.01; *** = <0.001.

Factors affecting how long subordinate females allonursed

The body condition of allolactators (weight relative to age) was an important predictor of how long they allonursed: subordinate female allolactation duration correlated positively with their mass relative to their age (Table 3; Fig. 4). Maternal body condition was also an

important predictor of allolactation duration: subordinate females also nursed for longer if the litter mother was relatively light for her age. Litter size was also significant in the best model, which suggests that females allonurse larger litters for longer periods. The number of allolactators nursing a litter did not predict how long each female individually nursed, and females did not nurse litters more closely related to them for longer periods.

DISCUSSION

Our results show that allolactation in the meerkat is most commonly associated with pregnancy, or the recent termination of a pregnancy. Pregnant and recently pregnant females may be physiologically primed for maternal care by their own pregnancy, resulting in hormonal sensitivity to the continued presence of another female's pups (Bridges 1996). During pregnancy, levels of prolactin, which promotes maternal care and lactation, increase by up to twenty times in mammalian females (Falconer 1980). This may explain incidences of allolactation pre-parturition, which is also seen in macaques (Tanaka 2004). Prolactin levels remain elevated for two weeks following the death of a neonate in tamarins (Ziegler 2000), indicating the potential for a hormonal predisposition during the post-abortion period toward allomaternal behaviour. Allo-nursing following the loss of a neonate has been observed in galagos (Kessler & Nash 2010) and Northern Elephant seals (Riedman & Le Bouef 1982). Prolactin release can be stimulated by offspring contact in non-pregnant rats (Sugiyama et al. 1996), suggesting the potential for a link between prolactin and allomaternal behaviour in non-pregnant as well as pregnant females. Elevated levels of prolactin in non-breeding helpers during the post-partum period are associated with parental care behaviours in cooperatively breeding birds (Schoech et al. 1996) and callitrichid monkeys (Ziegler et al.

1996; Mota & Sousa 2000). Prolactin plays a role in pathogen resistance, and delays fertility - an alternative hypothesis is that allolactation may not be a result of high prolactin levels, but a means of maintaining them to gain these benefits (Roulin & Hager 2003). Physiological readiness to lactate may also explain why litters born late in the season were more likely to be allonursed than those born at the beginning of the breeding season. Subordinate breeding is strongly influenced by rainfall (Clutton-Brock et al. 2001b), and rainfall increases as the breeding season progresses (Russell et al. 2002). Later in the season, there is therefore a higher likelihood that there will be pregnant or recently pregnant subordinate females in the group, which our results suggest are more likely to allonurse.

If females are physiologically primed for maternal behaviour by pregnancy, allolactation may arise simply as a by-product of this temporary condition rather than an adaptive investment. Allolactation in this case may be more comparable to milk-stealing, unintentional allonursing seen in a number of species (Murphey et al. 1995; de Bruyn et al. 2010), or milk-dumping, where females appear to readily give up milk not consumed by their own offspring. Milk-dumping is thought to explain allonursing in evening bats (Wilkinson 1992), and in grey seals (Beck et al. 2000). In both of these cases, however, evacuating excess milk reduces weight loads which increases flying and swimming efficiency – crucially important adaptive pressures which reduce the costs of lactation. Quantification of the benefits of allolactation for meerkat females could illuminate whether these benefits might overcome the substantial costs (Scantlebury et al. 2002) to make milk-evacuation, passive or active, a plausible explanation for the maintenance of this behaviour.

More pregnant and recently pregnant females allolactated for close relatives, suggesting that females may gain indirect benefits from allonursing. Kin-directed allonursing in singular breeders has also been shown in the dwarf mongoose: females which suckled the young of the sole breeding female were all her daughters or sisters (Rood 1980). Evidence of

kin discrimination suggests that kin selection plays a role in allolactation. However, within-group female relatedness in meerkats is high (0.41 ± 0.17 in this study), meaning that kin selection is still likely to explain allolactation in non-pregnant female meerkats, though they did not display selective nursing. As only one meerkat female breeds per group, meerkat females are at low risk of allonursing an unrelated infant (Clutton-Brock et al. 1999a). The increased sensitivity to relatedness of pregnant and recently pregnant females may be due to the extra costs of gestation (Gittleman & Thompson 1988; Rogowitz 1996), or the physiological stress associated with abortion (Arck et al. 2007), increasing the benefits of discriminating towards close kin.

Females which had recently been evicted from the group allolactated at a higher frequency than non-evicted females. Evictees separated from the group suffer considerable stress, weight loss, and reduced survival (Young et al. 2006). If contributing to allomaternal care allowed evicted females renewed access to the social group, there would be an incentive to do so in accordance with the “pay-to-stay” hypothesis (Gaston 1978). Increased helping effort following a separation from the group is seen in the cooperatively breeding cichlid species *Neolamprologus pulcher*: temporarily removed helpers subsequently increased their helping effort, and consequently aggression toward them was reduced (Balshine-Earn et al. 1998; Bergmüller & Taborksy 2005). A similar reduction in agonistic interactions between the dominant female and returning helpers is also seen in the meerkat (Young et al. 2006; Clutton-Brock et al. 2008). Helping as payment of “rent” is also suggested to be a likely explanation for the evolution of alloparental care in bird species where helpers similarly receive greater benefits from remaining in their natal territories due to a lack of opportunities to procure mates or territory elsewhere (Cockburn 1998). Investigation of whether dominant females discriminate between returning females that allonurse and those that do not would illuminate whether the pay-to-stay hypothesis could explain allolactation in this species. If so,

aggression towards returning females that subsequently allonurse should be less than towards females which return and do not.

Female body condition was not associated with female allolactation likelihood, but did predict how long allolactating females nursed litters, suggesting that the level of investment, but not the decision to invest, is condition-dependent. This contrasts with other studies of cooperative behaviours in meerkats which have shown that helping is condition-dependent: individual contributions to other allomaternal behaviours is influenced by weight (Clutton-Brock et al. 2002) and nutritional status (Clutton-Brock et al. 2001a). That allolactation does not appear to be condition-dependent in the meerkat suggests that the maintenance of this form of alloparental behaviour may be driven by different selection mechanisms. Allolactation duration correlated positively with litter size. Litters born to light females were also nursed for longer periods. Larger litters may generate increased rates of begging, increasing the perceived need of the litter (Manser et al. 2008) and leading to an increase in provisioning in meerkats (Madden et al. 2009). The negative correlation between maternal condition and the likelihood and duration of subordinate allolactation suggests that the perceived need of the litter does predicts a female's likelihood of providing allomaternal care. This is not linked to the positive correlation with litter size, as larger litters are usually produced by heavy females (Russell et al. 2003). Together these results could imply that allolactators may compensate for reduction of the mother's capacity for investment. Helper compensation has been demonstrated in superb fairy wrens (Russell et al. 2007a) and carrion crows (Canestrari et al. 2001), where mothers actively reduce investment in their eggs according to the number of helpers present. To our knowledge, however, elevation of alloparental behaviours as a compensatory response to low maternal quality has not previously been shown.

The occurrence of allolactation and how much meerkat females invest are driven by a complex combination of variables, including age, time in the season, litter size, and the body condition of both mother and lactator. This study's correlative findings suggest the need for further work. For example, investigation of levels of aggression from the dominant female toward allolactators and non-allolactators would illuminate the costs of not investing in pup care via allolactation, and the benefits of avoiding punishment, should it exist. That allolactation is more frequent for litters which are more likely to have greater need of extra care suggests that allolactation is beneficial for offspring and mother. Further work should quantify these benefits, including the long term consequences of receiving allolactation for pup and mother in terms of survival, reproductive success, and the potential transfer of immune compounds. Additional analysis of the costs and benefits to allolactators will further illuminate the selective advantages of this behaviour.

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Appendix 1. AIC_c ranked candidate model set showing relative importance of the following parameters on whether a dominant litter received allomaternal care in the form of allolactation or not: litter order within season within group, litter size, maternal weight at conception, and rainfall in month prior to litter birth.

Model	Parameters (<i>k</i>)	log likelihood	AIC _c	Δ _i	ω _i
litter order	3	-135.06	276.22	0.00	0.45
litter order, rainfall	4	-134.85	277.88	1.66	0.19
litter order, maternal weight relative to age	4	-134.85	277.89	1.67	0.19
litter order, group size	4	-135.01	278.20	1.98	0.17

Submodels were derived from a global model using a cut off of 2AIC_c greater than the best fitting model. Litter mother identity (n=47) was included as a random term in each model.

Appendix 2. AIC_c ranked candidate model set showing relative importance of the following parameters on how long (days) subordinate females allonursed: litter size, lactator weight relative to age, maternal weight relative to age, how many allolactators are nursing the same litter, and the lactator's relatedness to the litter mother.

Model	Parameters (<i>k</i>)	log likelihood	AIC _c	Δ _i	ω _i
lactator mass relative to age, maternal weight relative to age, litter size	5	-479.68	972.09	0.00	0.54
allolactator number, lactator mass relative to age, maternal weight relative to age, litter size	6	-479.39	973.77	1.68	0.23
lactator mass relative to age, maternal weight relative to age	4	-481.67	973.87	1.78	0.22

Submodels were derived from a global model using a cut off of 2AIC_c greater than the best fitting model. Litter mother identity (n=38) was included as a random term in each model.