No apparent benefits of allonursing for recipient offspring and mothers in the cooperatively breeding meerkat

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Running headline: No benefits of allonursing in meerkats?

Summary:

1. Cooperative behaviours by definition are those that provide some benefit to another individual. Allonursing, the nursing of non-descendent young, is often considered a cooperative behavior and is assumed to provide benefits to recipient offspring in terms of growth and survival, and to their mothers, by enabling them to share the lactation load. However, these proposed benefits are not well understood, in part because maternal and litter traits and other ecological and social variables are not independent of one another, making patterns hard to discern using standard univariate analyses.
2. Here, we investigate the potential benefits of allonursing in the cooperatively breeding Kalahari meerkat, where socially subordinate females allonurse the young of a dominant pair without having young of their own.
3. We use structural equation modelling to allow us to account for the interdependence of maternal traits, litter traits and environmental factors.
4. We find no evidence that allonursing provides benefits to pups or mothers. Pups that received allonursing were not heavier at emergence and did not have a higher survival rate than pups that did not receive allonursing. Mothers whose litters were allonursed were not in better physical condition, did not reconceive faster, and did not reduce their own nursing investment compared to mothers who nursed their litters alone. These patterns were not significantly influenced by whether mothers were in relatively good, or poor, condition.
5. We suggest that allonursing may persist in this species because the costs to allonurses may be low. Alternatively allonursing may confer other, more cryptic, benefits to pups or allonurses, such as immunological or social benefits.

Keywords: allonursing, cooperation, maternal condition, structural equation modeling, *Suricata suricatta*

Introduction

Cooperative behaviours by definition are those that provide some benefit to another individual, and this benefit is a fundamental assumption of hypotheses regarding their evolution (West et al. 2007; Cockburn et al. 2008). Although studies have demonstrated that the presence of cooperative "helper" individuals benefits breeders in a number of cooperatively breeding species (Hatchwell 1999; Gilchrist 2007; Russell et al. 2007; Cockburn et al. 2008), the benefits to recipients of individual cooperative behaviours are poorly understood, in part due to difficulties in separating the effects of cooperative behaviours from other related factors (Cockburn et al. 2008). As a result, some behaviours might be classified as cooperative without evidence supporting the key assumption that the behaviour provides benefits and has evolved at least partly due to this benefit.

Allonursing, the nursing of non-descendent young, is frequently assumed to be a cooperative behaviour, but may be at risk of misclassification in some species as the driving factors in its evolution remain unclear (Hayes 2000; Roulin 2002). Allonursing is widespread in mammals where females live in stable groups (Packer et al. 1992) despite lactation carrying a substantial energetic cost (Clutton-Brock et al. 1989). Hypotheses regarding the evolution of allonursing fall into two groups centered around its potentially cooperative nature. Perhaps the most intuitive interpretation of allonursing is that it is a cooperative behaviour, the evolution of which has been driven at least partly by benefits to recipients (Hayes 2000; Roulin 2002). Offspring may benefit in terms of growth and survival (König 1997; König et al. 2006) as milk is often the sole source of nutrition in early life (Loudon 1985). Mothers of allonursed young also may be likely to benefit in terms of physical condition and future reproductive success through sharing the lactation load with other females. Such benefits to recipients may result in indirect genetic benefits for females that nurse kin (Hayes 2000; Roulin 2002). Alternatively, allonursing might be a behaviour that is not actively cooperative in nature and does not necessarily benefit recipients. For example, milk might be "dumped" by females with excess, or might be stolen by non-offspring as a result of misdirected parental care (Hayes 2000; Roulin 2002). Understanding whether allonursing provides benefits to recipients is crucial to understanding whether and in which circumstances allonursing can be considered a cooperative behaviour.

Quantifying the benefits associated with cooperation is difficult, in part because the presence of helpers is often associated with other factors that might confound any beneficial effect, such as territory quality or size (Cockburn et al. 2008). This is also true of allonursing, which is most common in species that breed communally; here, incidences of allonursing commonly coincide with incidences of communal nesting (Hayes 2000), the benefits of which possibly confound any beneficial effects of allonursing. For example, comparisons of communally nursing groups to singly nursing females that nest alone have suggested that allomaternal rearing, including allonursing, provides benefits to both offspring and mothers in communally breeding rodents (Hayes & Solomon 2004; König et al. 2006, Auclair et al. 2014). However, interpretation of these results in terms of the benefits of allonursing specifically may be subject to flaws inherent in the paired comparisons methodology

(Dickinson & Hatchwell 2004), as any benefits of allonursing are likely to be closely linked to the benefits of communal nesting and group living, for example, increased thermoregulation (Hayes & Solomon 2004). An additional challenge in quantifying the benefits of a behaviour such as allonursing for recipient offspring and mothers is that offspring traits are often influenced by maternal body condition or age (Mousseau & Fox 1998), and both maternal and offspring traits can be sensitive to environmental and social factors. Determining the benefits of allonursing when many of the measured variables are influenced by common factors is clearly a challenge, as the interconnected nature of the data might obscure patterns and make it impossible to tease apart the role of allonursing using traditional univariate statistical analyses. Thus, although allonursing seems likely to convey a variety of benefits to recipients, these benefits, and therefore the cooperative nature of this behaviour, remain unclear.

In this study, we investigate the potential benefits of allonursing to offspring and mothers in the cooperatively breeding Kalahari meerkat (*Suricata suricatta*). In this species behaviourally subordinate females regularly allonurse the young of a dominant pair while rearing no offspring of their own (though subordinate females may occasionally breed) (MacLeod et al. 2013). Allonursing is most commonly undertaken by females that have recently lost litters of their own as a result of infanticide or recent eviction by the dominant female (MacLeod et al. 2013), though spontaneous lactation has also been reported (Doolan & Macdonald 1999). Allonursing has the potential to provide substantial benefits to both offspring and mothers in the meerkat. Offspring mass influences survival to independence (Russell et al. 2002), suggesting a role for extra nutrition through allonursing in determining survival and recruitment. Dominant mothers are also likely to benefit as the presence of non-lactating helpers reduces maternal energetic costs in meerkats (Scantlebury et al. 2002): the energetic demands on dominant mothers could thus be further reduced by allonurses sharing the burden of lactation, resulting in increased maternal condition post-lactation. Interbirth intervals have been shown to be positively correlated with maternal effort (Silk 1988), and negatively correlated with maternal condition (Hendrickx & Dukelow 1995). It is therefore likely that mothers whose litters are allonursed are able to reconceive faster and are in better condition than mothers whose litters are not allonursed.

The Kalahari meerkat system is uniquely suited to examine the benefits of allonursing for two major reasons. First, the allonursing recipient and donor roles are clear-cut as the litter born to the dominant female is most commonly the only litter being raised at any time (Clutton-Brock et al. 1998). Thus, allonursing is not reciprocal among females and any benefits of allonursing are not confounded with the simultaneous costs of also providing allonursing (mothers), or having maternal resources diverted to other young (offspring). This allows us to more clearly determine the extent to which offspring and mothers benefit from the presence of allonurses. Second, problems associated with a paired comparison methodology do not apply, as allonursing probability in this species is not associated with indicators of territory, environmental, or maternal quality (group size, maternal condition, rainfall), and allonursing and non-allonursing females exist in the same group (MacLeod et al. 2013). Thus, comparisons between litters that did and did not receive allonursing are unlikely to be confounded by other factors. To test predictions that allonursing should result in larger offspring that are more likely to survive to independence, and that dominant mothers whose litters are allonursed should be in better body condition after lactation, and have a reduced time to reconception, we use structural equation modelling and data from a long-term field project. While univariate analyses can provide information about how specific variables are associated, by taking a multivariate approach we can examine and disentangle the relationships among many interdependent variables, a previous constraint on estimating the benefits of cooperative behaviors and helpers (Cockburn et al. 2008).

Methods

We created a general framework (Fig. 1) relating allonursing, maternal and litter traits, and environmental factors. We used this framework to create a hypothesized a priori structural equation model to investigate whether the presence of allonursing influences maternal traits (physical condition, interbirth interval, lactation duration) and litter traits (average emergence weight, average survival to independence). Our framework also included expected relationships between maternal and litter traits. Primarily, we predicted that if a litter was allonursed, its mother might reduce her own lactation duration, resulting in better physical condition post-lactation, and reduced interbirth intervals. We also predicted that allonursing should benefit pups by increasing offspring size and, indirectly, survival. We also expected that several variables associated with both the abiotic environment (rainfall: Hodge et al. 2009) and the social environment (group size: Russell et al. 2002) would influence maternal condition. Maternal condition in turn was likely to influence litter traits such as litter size, average emergence weight, and proportion litter survival.

Data collection

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. The study population observed over this period included over 40 social groups; our dataset includes litters born in 22 of these groups. Groups were visited every 1-3 days. All individuals were habituated to close human proximity (<1 m), and were easily identifiable by unique dye-mark patterns (Hodge et al. 2008). The majority of individuals (>95%) were able to be voluntarily weighed on electronic scales (±1g) (Clutton-Brock et al. 2004). Individuals were weighed before they commenced foraging in the morning. Dominance rank is easily detected, as dominant females are the primary breeders in the group, and other individuals are behaviourally submissive to her. The dataset we used contained only litters born to dominant females and these were the only litters being raised by the group at that time. While subordinate females may occasionally breed, no subordinate litters are included in this analysis, and allonurses in this dataset were not concurrently nursing young of their own. Litters born to dominant females were given a binary code identifying whether they were nursed by more than one female (allonursed - "1"), or only by their mother (not allonursed - "0"). Lactation is easy to detect both in mothers and allonurses due to the obvious presence of damp, sandy rings around the nipples of lactating females (MacLeod et al. 2013).

Meerkat pups are born in an underground burrow, where they remain until they emerge at approximately three weeks of age. 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. Emergence weights were calculated for each pup by averaging all weight measurements collected before 1 month of age; from this data we calculated the mean emergence weight for each litter. Whether a pup survived to independence (3 months of age) was determined; from this data we determined the proportion of surviving offspring per litter (number of survivors to 3 months/litter size).

Maternal condition at conception was calculated as the residuals of conception biphasic growth model (English et al. 2012). It is therefore a measure of how heavy the female was for her age, relative to other females in the population. Females with positive residual values are in relatively good condition, and females with negative residual values are in relatively poor condition. Conception date was estimated by back-dating the length of gestation (70 days: Russell et al. 2002) from birth of a litter. Maternal mass at conception was the mean of the female's pre-foraging mass records in the week after the conception date. Maternal age was measured in days from the date of her birth to the date of conception. Maternal condition at the end of lactation was calculated in the same way, using the mean of the female's pre-foraging mass records in the week after she stopped lactating, and her age on the last day of lactation. Post-lactation weight is obviously affected if females reconceive during lactation – as we were testing effects on interbirth interval we could not standardize this measure by omitting any females that were pregnant again during this time from this analysis. However, as there is no discernible weight gain during the first month of pregnancy (Sharp et al. 2013), early pregnancy should not have a strong effect on post-lactation condition.

Maternal lactation duration was calculated as the time in days between the recorded onset and cessation of lactation. Lactation periods artificially shortened by the death of a litter or mother were not included in the analyses (N=306 excluded). 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, N=89), or where an allolactation period overlapped with lactation for the female's own litter (N=5), were excluded from analyses. Resultantly all records of lactation duration used in the analyses were accurate to within a week. Interbirth interval was defined as the time in days between the birth of a current litter, and that of a subsequent litter. Although meerkats can potentially breed year round, there is a substantial drop in births between May-July and a peak in births in Nov-Dec. We thus deemed the reproductive season to begin in July, and litters born from July onward were the first of the season. We excluded interbirth intervals that spanned reproductive seasons (i.e., between litters born at the end of one season and those born at the beginning of the next), as the length of these periods is likely to be driven primarily by environmental variables.

Rainfall is an established proxy for resource availability in this system (Hodge et al. 2009), and accounts for effects of environmental and seasonal variation. For each litter, we calculated average daily rainfall (ml) between litter conception and birth. We also include litter order (within the group, within the season) to account for variation according to time in the season that might not be explained by rainfall. Group size was defined as the total number of adult individuals (older than 6 months of age) present in the group on the litter's birthdate.

In total, we had complete data on 120 different litters from 39 females across 12 years. Of these 120 litters, allonursing occurred in 58 litters which is consistent with frequencies seen in larger samples (MacLeod et al. 2013). Ranges, means, and standard deviation values are reported for all variables in the model in Supplementary Table 1.

Statistical analysis

We used structural equation modelling (SEM) to examine how environmental variables and allonursing influenced maternal and litter traits. Structural equation modelling is particularly useful when variables are not independent of one another and can quantify the direct and indirect effects of factors while holding other factors constant (Grace 2006; Grace 2008). We used AMOS (Arbuckle 2006) to create our *a priori* hypothesized model and assess its adequacy (confirmatory analyses sensu Grace 2006; Grace 2008). We did not remove any non-significant relationships from the hypothesized model. We included curved lines without arrows between the errors of the following variables that we predicted to be strongly correlated with one another (i.e., covariance between residuals): condition of mothers pre-conception and post-lactation; rainfall and litter order; and number of offspring in a litter and the average mass of an offspring at emergence. Transformation of variables was determined based on the assessment of normality in AMOS to ensure that the data were approximately multivariate normal. Most variables were untransformed except for rainfall, interbirth interval and emergence weight which were natural log-transformed. We added one to rainfall values to account for zero values prior to transformation.

We compared the fit of our *a priori* hypothesized model to the fit of two alternative models. First, to examine whether including allonursing was an important component of the model (whether it improved the fit of the model), we compared our hypothesized model (with allonursing included) to an alternative 'allonursing excluded' model where the binomial 'allonursing' variable and all of its relationships were removed. Second, to examine whether there were maternal influences across years particular to the identity of the mother, we compared our hypothesized model (without mother identity) to an alternative model including mother identity as an observed variable. In this alternative 'mother identity included' model, mother identity connected the following variables: maternal condition pre-conception, maternal condition post-lactation, lactation duration, average emergence mass, litter size and proportion survival.

To examine whether the nature and extent of effects of allonursing depends on maternal condition, we again used our *a priori* hypothesized model but instead of treating all mothers as part of a single group (as described above), we separated mothers into two groups based on their pre-conception condition. Mothers with positive residuals pre-conception were included in the 'good condition' group (N = 68) and mothers with negative pre-conception residuals were included in the 'poor condition' group (N = 52). We specified these two groups in the data structure and reran our *a priori* hypothesized model. In so doing, the relationships among the factors in the model are free to vary between the maternal condition groups (i.e. no constraints) although a single model is fit to the dataset. We then compared our hypothesized model with no constraints to a model where we constrained the relationships with allonursing to be equal between our maternal condition groups. In other words, we specified four constraints and constrained the regression weights between allonursing and 'maternal lactation duration', 'litter order', 'post-lactation maternal condition' and 'mean litter emergence weight' to be equivalent between good and poor quality mothers. By comparing the unconstrained and constrained models, we can examine whether the relationships with allonursing are significantly different between mothers of good versus poor condition. If, for example, there are benefits of allonursing for poor quality mothers but not for good quality mothers, then we should find a significant difference between these models, with the constrained model being unsupported.

In comparing models, we subtracted the Chi-square value of our *a priori* hypothesized model from that of the alternative model and determined whether this difference was statistically significant at the difference in degrees of freedom between the two models (Grace 2006). Standardized regression weights (henceforth S.R.W.'s) are reported for relationships between variables in our hypothesized model. These estimates can be interpreted as the strength of an association and indicate how changing a variable by 1 standard deviation would impact another connected variable (in standard deviations) while holding all other variables constant.

Results

The *a priori* hypothesized structural equation model fit the data adequately and was not rejected (Table 1, Fig. 2). Allonursing did not have a significant effect on any of the paths specified in our hypothesized model: comparing the hypothesized model to the alternative 'allonursing excluded' model indicated that the models did not differ significantly from one another (χ^2 difference = 1.849, df = 6, P = 0.933). The alternative 'allonursing excluded' model fit the data adequately and was in fact a better fit to the data than our hypothesized model including allonursing (according to AIC), suggesting that allonursing did not affect patterns in the hypothesized model substantially (Table 1). Inclusion of maternal identity and its connections to maternal and litter traits significantly reduced model fit compared to the hypothesized model (χ^2 difference = 15.139, df = 5, P = 0.010) and did not adequately fit the data (Table 1).

The comparison between the models with and without allonursing suggests that the presence of allonursing did not contribute significantly to the overall patterns in the model. The weak effect of allonursing is further confirmed by examining its influence on both maternal and litter traits (Fig. 2). Allonursing did not strongly affect average pup emergence weight (S.R.W.= -0.11, $P = 0.137$), or influence pup survival indirectly (S.R.W. = -0.01). The presence of allonursing had its strongest influence on the body condition of mothers post-lactation with mothers being in lower condition after nursing if their litters had been allonursed, though these effects were weak and marginally not significant (S.R.W. = -0.14, $P = 0.052$). The presence of allonursing did not correlate with the lactation duration of mothers (S.R.W. = -0.06, $P = 0.480$). Allonursing had only a very small indirect effect on interbirth interval (S.R.W. = 0.07) through its effects on post-lactation maternal condition and lactation duration. Allonursing was more likely to occur for later litters (S.R.W. = 0.21; $P = 0.018$), which tended to be larger (S.R.W. = 0.43; $P < 0.001$).

Maternal condition at conception was not associated with how long mothers nursed the litter (S.R.W. = 0.01, $P = 0.938$). However, mothers that had nursed for longer were significantly heavier at the end of lactation (S.R.W. = 0.18, $P = 0.014$), and mothers in good condition after lactation reconceived faster (S.R.W. = -0.51, $P < 0.001$). Pup weight at emergence was strongly positively associated with maternal condition: mothers that were heavier after lactation had larger pups (S.R.W. = 0.38, $P < 0.001$). Pups were more likely to be small at emergence when they had been nursed for longer periods by their mother (S.R.W. = -0.29, $P < 0.001$). Measures of maternal condition were more strongly influenced by environmental factors than by the presence of allonursing: higher rainfall and larger groups were associated with poorer maternal condition pre-conception (rainfall: S.R.W. = -0.20, $P = 0.019$; group size: S.R.W. = -0.15, $P = 0.035$). Higher rainfall was also weakly associated with shorter interbirth intervals and lower pup survival although neither relationship was significant (interbirth interval: S.R.W. = -0.14, P = 0.066; pup survival: S.R.W. = -0.19, P = 0.081).

The benefits of allonursing (or lack of) did not strongly depend on maternal body condition. The fit of the hypothesized model and the relationships among the factors were similar regardless of whether we included all mothers in a single group (Table 1) or separated them into two groups based on their pre-conception condition (no constraints: χ^2 = 57.664, d.f. = 52, P = 0.274, CFI = 0.97, RMSEA = 0.030, AIC = 261.66). Importantly, the relationships with allonursing did not differ significantly between mothers of relatively good and poor pre-conception condition and the constrained model adequately fit the data (paths with allonursing constrained: χ^2 = 59.636, d.f. = 56, P = 0.345, CFI = 0.981, RMSEA = 0.023, AIC = 255.64). Allowing the relationships with allonursing to vary freely between good and poor quality mothers did not substantially improve the model over a constrained model (χ^2 difference = 1.714, df = 4, P = 0.788).

Discussion

We found no evidence to suggest that allonursing significantly benefits pups in terms of increasing their weight at emergence or survival, or that allonursing significantly benefits mothers in terms of reducing their lactation duration or interbirth intervals, or boosting their physical condition. Instead, litter traits and maternal reproductive decisions were strongly affected by maternal condition (independent of identity), which was itself strongly influenced by environmental factors. Furthermore, the patterns with allonursing did not differ substantially between mothers in relatively good condition and those in relatively poor condition. These results suggest that in this species, allonursing does not meet the definition of a cooperative behaviour (West et al. 2007). If allonursing does not have measurable benefits for pups or mothers, why then does it occur so regularly (~50% of litters)? We suggest three possible, and non-mutually exclusive, reasons for why allonursing might occur in this species: it may incur little cost, it may provide allonurses with social benefits, or the benefits of allonursing to recipients may be cryptic.

Allonursing may occur in the meerkat not because it is beneficial to pups or mothers, but because the costs are low for subordinate females. Meerkat females are more likely to allonurse when they have lost litters of their own and have excess milk (MacLeod et al. 2013). Allonursing is similarly suggested to occur in lions when females have excess milk as a low-cost by-product of crèching (Pusey & Packer 1994). For example, female lions tend to nurse non-offspring when their own offspring are older and have less need of it, and when their own litters are small. The "dumping" of excess milk not consumed by a female's own offspring is also thought to play a role in the evolution of allonursing in bats and seals (Wilkinson 1992; Beck 2000). These results are in line with comparative analyses across mammalian species where indirect benefits from allonursing are likely, that suggest that allonursing has evolved where the costs are low (MacLeod & Lukas 2014).

Allonursing may also confer social benefits to the allonurse without necessarily benefitting offspring or mother. For example, tufted capuchin (*Cebus nigritus*) females preferentially nurse the offspring of dominant females, possibly to gain social benefits such as increased tolerance or willingness to share resources by the dominant female (Baldovino &

Di Bitteti 2006). Subordinate female meerkats are more likely to allonurse if they have recently been forcibly evicted from the group by the dominant female, or if they have recently been pregnant (MacLeod et al. 2013), both conditions entailing sustained aggression from the dominant female (Young 2006). Allonursing to increase the tolerance of the dominant female may therefore be a beneficial strategy for females in these categories. This hypothesis, however, implies that not helping may result in punishment. There is no evidence for coercion of subordinate meerkat females by the dominant female (Santema & Clutton-Brock 2012), and evidence for punishment of lazy helpers is restricted to male helpers which "false feed" pups (Clutton-Brock et al. 2005). Thus, appeasement of the dominant female seems unlikely to be a main driving force behind subordinate allonursing in this species.

Alternatively, offspring may benefit from allonursing in cryptic ways not directly related to growth and survival: for example, by gaining immunological benefits from suckling from more than one female (Roulin & Heeb 1999). By receiving milk from a number of females, offspring may receive a wider range of immune compounds, boosting immunocompetence (Roulin & Heeb 1999). Although we did not see a difference in survival to independence, which could be influenced by these sorts of immunological benefits, it is possible that immunological benefits may only be detectable in adulthood when variation in survival may be greater. It would therefore be informative to look for long term effects of allonursing in adult individuals. A detailed analysis of milk composition and immune compounds would also provide information on whether allonursed pups do indeed receive a wider range of immune compounds compared to pups that only receive milk from their mothers.

Another possible cryptic benefit of allonursing is that it serves to soothe offspring after a stressful event. This is thought to be the case in tufted capuchin monkeys, where allonursing bouts are short and non-lactating females may also suckle young (Baldovino & Di Bitteti 2006); and in African elephants, where allonurses are most commonly nulliparous females that are unlikely to be transferring milk (Lee 1987). Non-nutritive suckling is widespread in mammals (Cameron 1998) and soothing offspring via non-nutritive suckling might possibly explain allonursing in non-pregnant meerkat females, which has been thought to represent spontaneous lactation (Doolan & Macdonald 1999). However, the majority of meerkat allonurses are females that have recently lost litters and so are likely to have excess milk. In these cases, it is likely that milk is being transferred during nursing, making it unlikely that soothing is the primary function of allonursing in meerkats. Whether and how much milk is transferred to offspring by non-pregnant females is necessary to determine the whether soothing offspring is a cryptic benefit of allonursing in this species.

Although non-significant, the apparent associations between allonursing and poor maternal condition post-lactation and low pup emergence weights are surprising. Despite the inferred directionality of the relationships in the model, these associations are correlative and do not necessarily indicate that allonursing has negative effects on maternal or litter traits. Instead, these negative associations are more likely indicative of allonursing being more common when mothers are in poor condition, and that initially small pups may be more likely to be allonursed. When mothers are in relatively poor condition, allonurses nurse for longer periods (MacLeod et al. 2013), indicating that allonurses may compensate for a reduced ability of mothers to invest in lactation. Evidence for allonursing as compensation for low birth weight and/or nutritional deficiency has been seen in cattle: calves with low birth weight and those which were suckled at a lower rate by their mother, suckled other females at a higher rate (Vichova & Bartos 2005). Likewise, guanaco calves which were allonursed had mothers with lower body weight than the mothers of calves that did not receive allonursing (Zapata et al. 2010). In this analysis, however, we do not see different relationships with allonursing for mothers in good versus poor condition, which might be expected if compensation for poor maternal condition was the primary function of allonursing in this species. Unfortunately the greatest potential compensatory effects on pup growth are likely to be seen before access to the pups is possible, as the average length of allonursing is around 30 days (MacLeod et al. 2013), and weight data for pups only begins to be collected around this time.

In contrast to the weak effects of allonursing, environmental factors had a strong effect on maternal condition. Maternal condition, unexpectedly, was poorest when mothers were in large groups and when rainfall was high. Subordinate female meerkats are more likely to breed, and be evicted, when rainfall is high, and groups are large (Clutton-Brock et al. 2001; Clutton-Brock et al. 2008). If the aggressive suppression of subordinate breeding carries a physical cost, as has been shown in a number of species (Hackländer et al. 2003; Bell et al. 2012), dominant female body condition could consequently be reduced in these circumstances. However, this hypothesis would rely on the costs of reproductive suppression being greater than any benefits accrued through the increased food availability shown to be associated with rainfall (Barnard 2000; Russell et al. 2002; Hodge et al. 2009), so this explanation remains speculative. Litter traits and maternal reproductive decisions were primarily influenced by maternal condition, rather than allonursing. Mothers in good condition reconceived quickly and produced large pups which consequently had higher survival to independence. Contrary to predictions, mothers that nursed their litters the longest were in the best condition after lactation. This result could indicate that the time spent nursing does not represent the cost of lactation or milk transfer (Cameron 1998).

A number of hypotheses for why females allonurse assumes that allonursing is a cooperative behavior and is associated with benefits to recipients. We examined potential direct and indirect benefits of allonursing in the meerkat to determine whether allonursing fits the definition of a cooperative behavior in meerkats. Our results, however, suggest that allonursing does not have a strong influence on the framework we investigated, and is not associated with clear physical benefits to pups or mothers. These results caution that the benefits of allonursing to recipients, and its potential cooperative nature, should not be assumed. Quantification of what, if any, benefits allonursing provides to recipients in other species would provide valuable insights into the evolution of this behaviour. Our multivariate structural equation modelling approach also unveils interesting patterns that may have been masked by a univariate approach: for example, though we would have predicted that high rainfall and large group size should positively influence offspring condition, these variables were negatively associated with maternal condition, which was the strongest predictor of offspring condition. This highlights the usefulness of a multivariate approach, especially when dealing with social behaviour where many variables are likely to be interdependent.

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Data accessibility

All data will, upon acceptance, be available on Dryad (DOI pending).

References

Arbuckle, J. L. (2006) Amos (Version 21.0) [Computer Program]. Chicago: SPSS.

Auclair, Y., König, B., Ferrari, M., Perony, N. & Lindholm, A.K. (2014) Nest Attendance of Lactating Females in a Wild House Mouse Population: Benefits Associated with Communal Nesting. *Animal Behaviour*, 92, 143–49.

Baldovino, M.C., and Di Bitetti, M.S. (2008) Allonursing in Tufted Capuchin Monkeys (*Cebus nigritus*): Milk or Pacifier? *Folia Primatologica*, 79, 79–92.

Barnard, J.A. 2000. *Costs and benefits of group foraging in cooperatively breeding meerkats.* PhD. Cambridge, UK: University of Cambridge.

Beck, C. A., Bowen, W. D. & Iverson, S. J. (2000) Seasonal Changes in Buoyancy and Diving Behaviour of Adult Grey Seals. *Journal of Experimental Biology*, 203, 2323–30.

Bell, M.B.V., Nichols, H. J., Gilchrist, J. S., Cant, M. A. & Hodge, S. J. 2012. The cost of dominance: suppressing subordinate reproduction affects the reproductive success of dominant female banded mongooses. *Proceedings of the Royal Society B: Biological Sciences*, 279, 619–624.

Cameron, E.Z. (1998) Is Suckling Behaviour a Useful Predictor of Milk Intake? A Review. *Animal Behaviour,* 56, 521–32.

Clutton-Brock, T.H., S.D. Albon & F.E. Guinness. (1989) Fitness Costs of Gestation and Lactation in Wild Mammals. *Nature,* 337, 260–62.

Clutton-Brock, T. H., D. Gaynor, R. Kansky, A. D. C. MacColl, G. McIlrath, P. Chadwick, P. N. M. Brotherton, J. M. O'Riain, M. Manser, and J. D. Skinner. (1998) Costs of Cooperative Behaviour in Suricates (*Suricata suricatta*). *Proceedings of the Royal Society B: Biological Sciences,* 265, 185–90.

Clutton-Brock, T. H., Brotherton, P. N. M., Russell, A. F., O'Riain, M. J., Gaynor, D., Kansky, R., Griffin, A., Manser, M., Sharpe, L., McIlrath, G.M., Small, T., Moss, A. & Monfort, S. (2001) Cooperation, Control, and Concession in Meerkat Groups. *Science,* 291, 478–81.

Clutton-Brock, T. H., Russell, A. F. & Sharpe, L. L. (2004) Behavioural Tactics of Breeders in Cooperative Meerkats. *Animal Behaviour,* 68, 1029–40.

Clutton-Brock, T. H, Russell, A. F., Sharpe, L.L. & Jordan, N.R. (2005) 'False Feeding' and Aggression in Meerkat Societies. *Animal* Behaviour, 69, 1273–84.

Clutton-Brock, T.H., Hodge, S., & Flower, T. (2008) Group Size and the Suppression of Subordinate Reproduction in Kalahari Meerkats. *Animal Behaviour,* 76, 689–700.

Cockburn, A., Sims, R. A., Osmond, H. L., Green, D. J., Double, M. C. & Mulder, R. A. (2008) Can we measure the benefits of help in cooperatively breeding birds: the case of superb fairy-wrens *Malurus cyaneus*? *Journal of Animal Ecology*, 77, 430–438.

Dickinson, J. L. & Hatchwell, B. J. (2004) Fitness consequences of helping. *Ecology and Evolution of Cooperative Breeding in Birds* (eds W. Koenig and J. L. Dickinson), pp48–66. Cambridge, UK; Cambridge University Press.

Doolan, S. P. & Macdonald, D.W. (1999) Co-Operative Rearing by Slender-Tailed Meerkats (*Suricata Suricatta*) in the Southern Kalahari. *Ethology*, 105, 851–66.

English, S., Bateman, A.W. & Clutton-Brock, T.H. (2012) Lifetime growth in wild meerkats: incorporating life history and environmental factors into a standard growth model. *Oecologia*, 169, 143–153.

Gilchrist, J.S. (2007). Cooperative behaviour in cooperative breeders: costs, benefits, and communal breeding. *Behavioural Processes*, 76, 100–105.

Grace, J. B. (2006) *Structural Equation Modeling and Natural Systems*. New York, Cambridge University Press.

Grace, J. B. (2008) Structural equation modeling for observational studies. *Journal of Wildlife Management*, 72, 14-22.

Hackländer, K., Möstl, E. & Arnold, W. 2003. Reproductive suppression in female Alpine marmots, Marmota marmota. *Animal Behaviour*, 65, 1133–1140.

Hatchwell, B.J. (1999) Investment Strategies of Breeders in Avian Cooperative Breeding Systems. *The American Naturalist*, 154, 205–219.

Hayes, L.D. (2000) To Nest Communally or Not to Nest Communally: A Review of Rodent Communal Nesting and Nursing. *Animal Behaviour,* 59, 677–88.

Hayes, L.D. & N.G. Solomon. (2004) Costs and Benefits of Communal Rearing to Female Prairie Voles (Microtus Ochrogaster). *Behavioral Ecology and Sociobiology,* 56, 585–93.

Hendrickx, A.G. & Dukelow, W.R. (1995) Reproductive biology. *Nonhuman Primates in Biomedical Research (*Eds. B. T. Bennett, C. R. Abee, and R. Henrickson), pp147 – 191. New York, San Diego: Academic Press.

Hodge, S. J., Manica, A., Flower, T. P. & Clutton-Brock, T. H. (2008) Determinants of Reproductive Success in Dominant Female Meerkats. *Journal of Animal Ecology,* 77, 92–102.

Hodge, S.J., Thornton, A., Flower, T.P. & Clutton-Brock. T.H. (2009) Food Limitation Increases Aggression in Juvenile Meerkats. *Behavioral Ecology*, 20, 930–35.

Iacobucci, D. (2010) Structural equations modeling: Fit indices, sample size, and advanced topics. *Journal of Consumer Psychology*, 20, 90-98.

König, B. (1997) Cooperative Care of Young in Mammals. *Naturwissenschaften,* 84, 95–104.

König, B. (2006) Non-Offspring Nursing in Mammals: General Implications from a Case Study on House Mice. *Cooperation in Primates and Humans: Mechanisms and Evolution* (eds P. M. Kappeler and C. P. van Schaik), pp191–208. Berlin, Germany: Springer-Verlag.

Lee, P.C. (1987) Allomothering among African Elephants. *Animal Behaviour*, 35, 278–91.

Loudon, A.S.I. (1985) Lactation and Neonatal Survival of Mammals. *Symposia of the Zoological Society of London*, 183–207.

MacLeod, K.J., Nielsen, J.F., & Clutton-Brock, T.H. (2013) Factors Predicting the Frequency, Likelihood and Duration of Allonursing in the Cooperatively Breeding Meerkat. *Animal Behaviour*, 86, 1059–67.

MacLeod, K.J. & Lukas, D. (2014) Revisiting non-offspring nursing: allonursing evolves when the costs are low. *Biology Letters*, 10, 20140378.

Mousseau, T.A. & Fox, C. W. (1998) *Maternal Effects as Adaptations.* Oxford, UK: Oxford University Press.

Packer, C., S. Lewis, and A. Pusey. (1992) A Comparative-Analysis of Nonoffspring Nursing. *Animal Behaviour*, 43, 265–81.

Pusey, A. E., & Packer, C. (1994) Non-Offspring Nursing in Social Carnivores: Minimizing the Costs. *Behavioral Ecology*, 5, 362–74.

Roulin, A. (2002) Why Do Lactating Females Nurse Alien Offspring? A Review of Hypotheses and Empirical Evidence. *Animal Behaviour*, 63, 201–8.

Roulin, A., and P. Heeb. (1999) The Immunological Function of Allosuckling. *Ecology Letters*, 2, 319–24.

Russell, A. F., Clutton-Brock, T. H., Brotherton, P. N. M., Sharpe, L. L., Mcilrath, G. M. F., Dalerum, D., Cameron, E. Z. & Barnard, J. A. 2002 Factors Affecting Pup Growth and

Survival in Co-Operatively Breeding Meerkats *Suricata Suricatta*. *Journal of Animal Ecology*, 71: 700–709.

Russell, A. F., Brotherton, P. N. M., McIlrath, G. M., Sharpe, L. L. & Clutton-Brock, T. H. (2003) Breeding Success in Cooperative Meerkats: Effects of Helper Number and Maternal State. *Behavioral Ecology*, 14, 486–92.

Russell, A.F., Young, A. J., Spong, G., Jordan, N. R. & Clutton-Brock, T. H. (2007). Helpers increase the reproductive potential of offspring in cooperative meerkats. *Proceedings of the Royal Society B: Biological Sciences*, 274, 513 –520.

Santema, P. & Clutton-Brock, T.H. (2012) Dominant Female Meerkats Do Not Use Aggression to Elevate Work Rates of Helpers in Response to Increased Brood Demand. *Animal Behaviour*, 83, 827–32.

Scantlebury, M., A. F. Russell, G. M. McIlrath, J. R. Speakman, & T. H. Clutton-Brock. (2002) The Energetics of Lactation in Cooperatively Breeding Meerkats Suricata Suricatta. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269, 2147–53.

Sharp, S.P., English, S. & Clutton-Brock, T.H. (2013) Maternal Investment during Pregnancy in Wild Meerkats. *Evolutionary Ecology*, 27, 1033–44.

Silk, J.B. (1988) Maternal Investment in Captive Bonnet Macaques (*Macaca radiata*). *The American Naturalist*, 132, 1–19.

Vichova, J., & Bartos, L. (2005) Allosuckling in Cattle: Gain or Compensation? *Applied Animal Behaviour Science*, 94, 223–35.

West, S.A., Griffin, A.S. & Gardner, A. (2007) Social semantics: altruims, cooperation, mutualism, strong reciprocity and group selection. *Journal of Evolutionary Biology*, 20, 415–432.

Wilkinson, G. S. (1992) Communal Nursing in the Evening Bat, *Nycticeius Humeralis*. *Behavioral Ecology and Sociobiology,* 31, 225–35.

Zapata, B., Correa, L. A., Soto Gamboa, M., Latorre, E., Gonzalez, B. A. & Ebensperger, L. A. (2010) Allosuckling Allows Growing Offspring to Compensate for Insufficient Maternal Milk in Farmed Guanacos (*Lama guanicoe*). *Applied Animal Behaviour Science,* 122, 119–26.

Young, A. J., Carlson, A. A., Monfort, S. L., Russell, A. F., Bennett, N. C. & Clutton-Brock, T. H. (2006) Stress and the Suppression of Subordinate Reproduction in Cooperatively Breeding Meerkats. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 12005–10.

Table 1. Chi-squared values and fit indices of our three candidate models. For a model to adequately fit the data, $P > 0.05$, and CFI > 0.95. Model (c) does not fit the data.

Model	χ^2	d.f.	P	CFI	RMSEA	AIC
a) Hypothesized model	29.995	26	0.268	0.982	0.036	131.99
b) ‘Allonursing excluded’ model	28.146	20	0.106	0.963	0.059	118.15
c) ‘Mother identity included’ model	45.134	31	0.049	0.939	0.062	163.13

CFI = Comparative Fit Index; RMSEA = Root Mean Square Error of Approximation; AIC = Akaike Information Criterion.

FIGURE HEADINGS

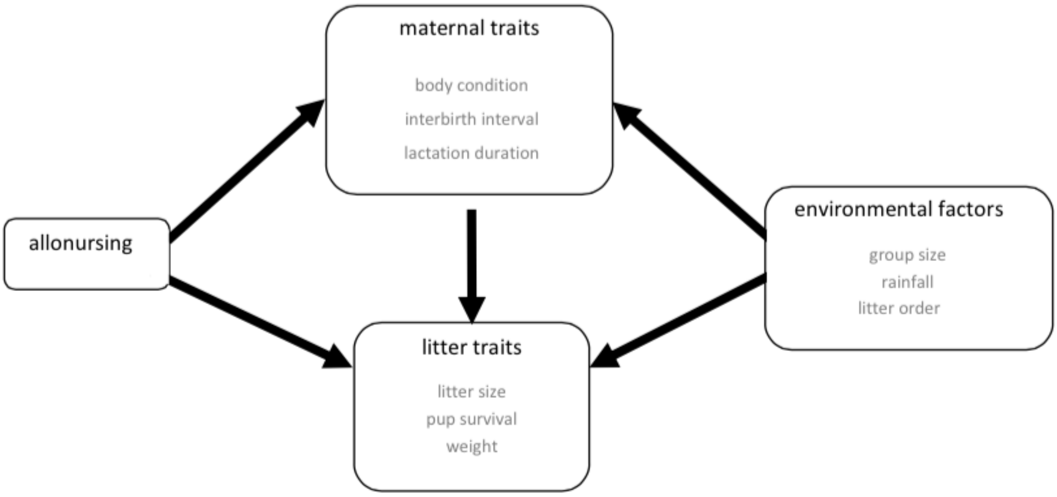


Figure 1. A general framework regarding associations of interest among environmental factors, maternal traits, litter traits and allonursing.

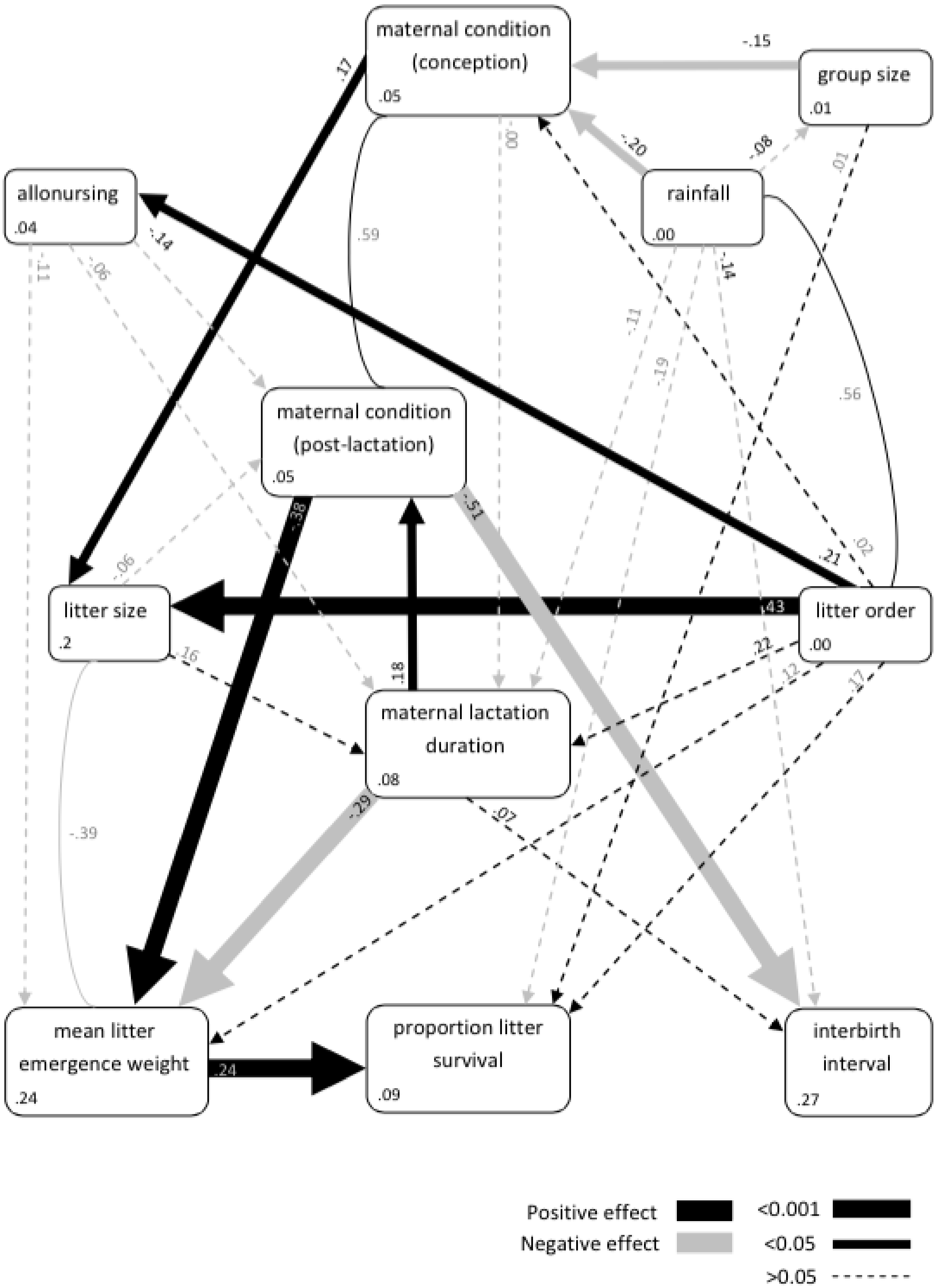
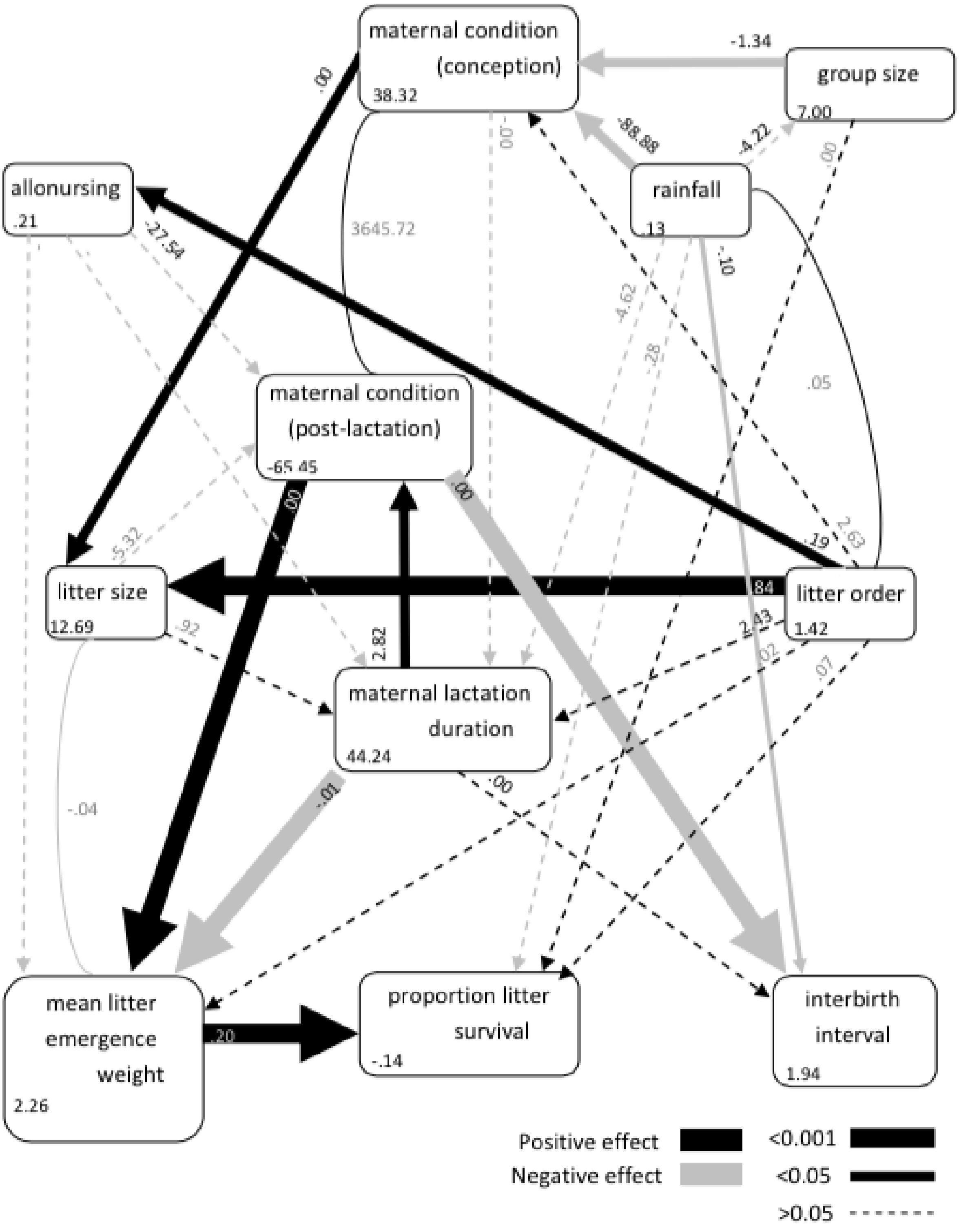


Figure 2. Path diagram for the *a priori* hypothesized structural equation model showing the standardized regression weights (measured in standard deviation units). Statistically significant paths are indicated by solid arrows ($P < 0.05$) with the strength of the relationships indicated by the width of the arrows and color indicating the direction (positive relationships in black and negative relationships in grey). Non-significant paths are indicated by dashed

arrows. Straight arrows reflect causal paths; curved lines without arrows indicate correlations. The values in the boxes indicate the amount of variation in that variable explained by the input arrows (R^2 values). N = 120 litters. (See supplemental Figure S1 for unstandardized coefficients).



Supplementary Figure 1. Path diagram for the hypothesized *a priori* structural equation model showing the unstandardized regression weights. Statistically significant paths are indicated by solid arrows (P < 0.05) with the strength of the relationships indicated by the width of the arrows and color indicating the direction (positive relationships in black and negative relationships in grey). Non-significant paths are indicated by dashed arrows. Straight arrows reflect causal paths; curved lines without arrows indicate correlations. The values in the boxes indicate the amount of variation in that variable explained by the input arrows (R^2 values). N = 120 litters.