Low costs of allonursing in meerkats: mitigation by behavioral change?

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Abstract

Allonursing, the nursing of another female's offspring, is assumed to impose a substantial energetic cost given the high cost of lactation to mothers. However, these costs have not been quantified. In cooperatively breeding mammals where helpers contribute to lactation, they might be expected to modify their behavior to mitigate these potential costs. Here, we show that overnight weight loss during lactation did not differ between allonurses and controls. However, meerkat helpers that allonursed do not gain weight over a reproductive bout as non-allonursing subordinate females did, suggesting that allonurses may incur some cost. Allonurses may mitigate the costs by increasing foraging effort during lactation. Allonurses do not, as expected, reduce investment in other cooperative behaviors during lactation. We suggest that the increase in cooperative behavior, including allonursing, may serve a social function, but further work is needed to confirm this hypothesis.

Key words: allolactation ; behavioral modification ; meerkat ; Suricata suricatta.

INTRODUCTION

Allolactation, or allonursing, is the nursing of nondescendent offspring (Packer et al. 1992; Roulin 2002). This form of alloparental care occurs across a diverse array of mammals, from cetaceans and canids to humans (Packer et al. 1992; Hewlett and Winn 2014), and is most common where multiple females breed at the same time and nest communally (Packer et al. 1992; Roulin 2002). Although in some cases, allonursing is best explained as nonadaptive misdirected maternal care or milk theft (Packer et al. 1992), there is growing evidence that allonursing is not simply a by-product of living in groups and is adaptive (Auclair et al. 2014; Weidt et al. 2014). Allonurses may benefit from diverting resources to nonoffspring: for example, nonoffspring nursing may be reciprocated by other mothers, a means by which inexperienced females gain experience in maternal care, or allonurses may gain indirect benefits from nursing related young (Hayes 2000; Roulin 2002). Allonursing is thought to convey a variety of benefits to offspring in terms of growth and survival (König 1997; König et al. 2006) and may also provide benefits to mothers of recipient offspring (Auclair et al. 2014). Despite the potential benefits to allonurses and recipient offspring and mothers, the nursing of nonoffspring is likely to impose substantial costs on allonurses, as lactation is the most costly aspect of maternal care (Clutton-Brock et al. 1989).

The costs of offspring care can negatively impact parental fitness, with long-term implications for the ability to invest in future offspring (Trivers 1972); the same is likely to be true for alloparents, including allonurses. In cooperatively breeding species, alloparents contribute to offspring care by defending, guarding, feeding, and, in mammals, carrying and nursing young (Riedman 1982; Cant 2012). These activities are likely to be energetically demanding, and a number of studies have produced evidence of costs associated with helping: for example, helpers suffer significant weight loss in white-winged choughs (Corcorax melanorhamphos) and alpine marmots (Marmota marmota) (Arnold 1990; Heinsohn and Cockburn 1994), and growth rates are reduced in cooperatively breeding cichlid helpers (Neolamprologus pulcher: Taborsky 1984). Long-term costs of helping behavior have also been demonstrated in the pied kingfisher (Ceryle rudis), in which high levels of investment in guarding nests and feeding young is associated with reduced survival and lowered chances of mating (Reyer 1984).

Adaptations to minimize the costs of offspring care while avoiding reduction in investment in the current brood would therefore be expected, for both mothers and alloparents. Several studies provide evidence that mothers mitigate the costs of care by downregulating noncare behaviors (McLean and Speakman 1997; Barrett et al. 2006) or increasing food intake (Goldizen 1987; Price 1992). Where helping is costly, helpers might also be expected to modify their behavior to mitigate the costs of offspring care. For example, a number of studies have shown that contributions to cooperative rearing may be condition dependent (Eden 1987; Boland et al. 1997; MacLeod et al. 2013). In addition, helpers might be expected to compensate for the costs of alloparental care by reducing investment in other costly behaviors or increasing food intake. However, investigation of potential behavioral modification in response to the costs of alloparental care has thus far been limited (Russell et al. 2003b). Furthermore, to our knowledge, there has been no investigation of behavioral modification in any species specifically in response to the costs of allonursing.

To determine whether helpers modify their behavior to mitigate the costs of allonursing first requires an understanding of how costly this behavior is. The costs of allonursing remain largely unquantified, as allonursing is most common in communally breeding species where all females nurse each other’s young: here, females are providing allonursing at the same time that their offspring are receiving it, so the benefits are likely to mask the costs, and vice versa. Less commonly, allonursing occurs in singular breeders where only one female produces offspring and allolactators do not have litters of their own, as in the dwarf mongoose (Helogale parvula: Creel et al. 1991) and the Kalahari meerkat (Suricata suricatta: MacLeod et al. 2013). In these cases, there is potential to disentangle the costs of allonursing from the benefits, as allonursing is not reciprocal, and so providers of allonursing are not simultaneously recipients.

Here, we investigate the costs of allonursing (the nursing of nondescendent offspring) to subordinate female meerkats and the behavioral responses of allonurses to the energetic costs they may incur. Kalahari meerkats (S. suricatta) are highly gregarious obligate cooperative breeders inhabiting semiarid regions of Southern Africa. In social groups of up to 40 individuals (but with a mean group size of 15), a socially dominant pair breeds, and subordinate individuals of both sexes help to rear their offspring (Doolan and Macdonald 1999). The dominant individuals produce over 80% of all offspring (Clutton-Brock et al. 1999; Griffin et al. 2003), but subordinates may occasionally breed. Subordinate pregnancies are rarely successful due to aggressive reproductive suppression by the dominant female (Young et al. 2006). Litters consist of, on average, 3–4 pups (MacLeod and

Clutton-Brock 2013). Pups are born and remain in an underground burrow until they are approximately 3 weeks old, after which they emerge and begin to forage with the group (Russell et al. 2002). During these periods, subordinate helpers will “babysit” young at their sleeping burrow during the day, and once the pups are old enough to join the group, provision them with food items until they are capable of foraging independently (Clutton-Brock et al. 2002). Independence is reached at around 3 months of age and adulthood at around 1 year. Adult mass is typically between 650 and 850g, but this is highly variable (English et al. 2012).

Our analysis investigates 3 questions. First, what are the costs of allonursing? A study investigating the costs of lactation in the meerkat found that in a small sample of allonurses, females lost weight during allolactation (Scantlebury et al. 2002), though this was attributed to increased rates of babysitting in these females. In this study, we also use weight loss as a proxy for lactation costs and attempt to disentangle the effects of allonursing on body mass from the effects of other cooperative behaviors. Body mass is a significant predictor of survival and fecundity of both dominant and subordinate female meerkats (Clutton-Brock et al. 2001; Russell et al. 2003a). Body mass also predicts the likelihood that a female will acquire the dominant breeding position (Hodge et al. 2008), which has substantial consequences for lifetime reproductive success as dominant females produce over 80% of all offspring within a group (Griffin et al. 2003). Weight loss therefore represents a significant cost in this species. Second, do meerkat females adjust their investment in foraging and noncare behaviors during lactation? A previous study has suggested that meerkat helpers may modify their behavior in the long term in response to the costs of babysitting and pup-feeding: helpers that invest heavily in babysitting and pup-feeding in a breeding event contribute less help in the next breeding event (Russell et al. 2003b)—though this may represent regression to the mean (i.e., if measurement of investment is extreme on first measurement, it will likely be closer to the average on next measurement). No studies, however, have investigated modifications in behavior in the short term, or in response to allonursing costs, which are unknown in this species. Third, do allonursing and non-allonursing subordinate females differ in investment in forms of cooperative behavior? We predict that allonurses incur significant costs, and that they mitigate these costs by increasing their foraging effort and reducing contributions to noncare cooperative behaviors, such as antipredator vigilance (Clutton-Brock et al. 1999) and burrow maintenance (Doolan and Macdonald 1999) during the period of lactation relative to non-allonursing subordinate females.

METHODS

Study population

Data were collected at the Kuruman River Reserve in the Kalahari region of South Africa (26°58′ S, 21°49′ E). All individuals were habituated to close human proximity (<1 m) and were identifiable by individually distinct dye-mark patterns which were applied and maintained while the animal rested (Hodge et al. 2008). All data collection was carried out in accordance with the guidelines of the University of Cambridge and the University of Pretoria. The Northern Cape Conservation Authority in South Africa provided permission to carry out the research.

The dominant female is the primary breeder in the group, and so dominance status is easily determined (Clutton-Brock et al. 1998). Individuals are weighed before the group begins foraging after emergence in the morning and in the evening after foraging has ceased. This is achieved without the need for capture using electronic scales onto which the animals are enticed using a small reward of water or hard-boiled egg (Russell et al. 2002). Pregnancies were easily detectable in their later stages due to weight increase, and birth dates could be identified to within 3 days, due to substantial changes in weight and appearance. Lactation was also 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 (MacLeod et al. 2013). 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.

We identified 3 periods of interest for comparison of rates of behavior and weight change. “Prelactation” was the 2-week period before a female starts to lactate or allonurse; “Lactation” was the period between the start and end of lactation or allonursing, the length of which varies according to the individual; and “Postlactation” was the 2-week period after a female ceases to lactate or allonurse.

Focal observations (Altmann 1974) were carried out between July 2009 and March 2010, July 2010 and March 2011, and August and December 2012 using 12 social groups. Focal observation sessions, each of 30min in length, were collected using Psion Organisers (Psion PLC) which record all behaviors to the nearest second. The behaviors of interest were as follows: foraging (committed digging in one spot with a radius of less than 15cm for more than 3 s); renovation of burrows or bolt-holes (to which meerkats flee upon hearing alarm calls); raised guarding (antipredator vigilance from an elevated vantage point, described in Clutton-Brock et al. 1999); resting (lying down, self-grooming, or a pause in foraging or moving that is not accompanied by obvious scanning of the surrounds); and pup-feeding (Clutton-Brock et al. 2002). Whether or not individuals remained at the burrow to babysit was also recorded in half-day sessions, confirmed by noting the babysitters’ remaining at the burrow after the group has left in the morning or presence at the burrow upon returning in the evening. Focal observations were carried out during periods of normal foraging. Observations were paused when normal foraging behavior ceased, usually in response to major alarm calls, encounters with other meerkat groups, or prolonged rests in extreme heat.

The costs of allonursing

As very little suckling of offspring is seen above ground during the day, it is assumed that suckling occurs primarily in the sleeping burrow overnight. To determine whether allonursing carries a cost in terms of weight loss, we tested 2 things: overnight weight loss during lactation and the overall weight change over a reproductive bout, with the predictions that allonurses should lose more weight overnight during lactation, and over the lactation period, than non-allonursing subordinate females.

All data for analysis of weight change or loss were collected between December 1996 and April 2011, during which time the study population included over 40 social groups. For each allonursing subordinate female, an adult (>1 year) non-allonursing subordinate female present in each group during these periods was randomly selected as a control by numbering females within a group and using a random number generator. There frequently was a lack of suitable control females in the same group as a corresponding allonurse due to small group sizes, pregnancy, or eviction. To widen the dataset while keeping consistent variables that might influence weight change, such as the social environment associated with the birth of a litter, we selected females randomly from across all groups. As some of these groups did not contain allonurses, we specified that control lactation period dates correspond to those of the dominant lactator of their group. This allowed us to compare rates of behaviors specific to the rearing of a litter, for example, pup-provisioning and babysitting. As pregnancy is likely to affect weight change over this period, subordinate females known to be pregnant or recently pregnant within a month of the prelactation date or during the pre- to postlactation period were excluded from allonurse and control samples.

We selected from adult subordinate females only to minimize differences in prelactation weight and social behavior between the 2 comparison groups (allonurses and non-allonursing subordinate females). However, it should be noted that control females were significantly lighter in the prelactation period than allonurses (mean allonurse weight: 657.6g ± 65.9; mean control weight: 594.6g ± 112.6; Student's T-test $T_{268} = -5.86$, $P < 0.01$) and were significantly younger than allonurses (mean allonurse age: 670.6 days ± 323.9; mean control age: 475.2 days ± 359.5; Kruskal–Wallis $\chi 2 = 56.08$, $P < 0.01$). This difference is consistent with previous results showing that allonurses are most commonly the oldest subordinate females in the group (MacLeod et al. 2013), and age is closely linked with mass (English et al. 2012). We control for this difference in our models, as discussed below.

Overnight weight loss

Overnight weight losses for dominant lactators, subordinate allonurses, and control females in the lactation period were calculated from evening-to-morning weight sequences in the database. For this analysis, we include dominant lactators primarily to test the assumption that lactating mothers should lose weight overnight when suckling is assumed to occur. We tested for differences between allonursing and non-allonursing control females in overnight weight loss by fitting weight loss as a response variable in Generalized Linear Mixed Models (GLMM) using the lme4 package in R (Bates et al. 2008), with allonursing status (allonurse, non-allonursing subordinate female) specified as a categorical explanatory variable. We specified female identity as a random term, as several females in the dataset nursed more than one litter or appeared as controls more than once. We controlled for the effect of environmental variation by including the average daily rainfall during the lactation period as an explanatory variable in the model, as rainfall is strongly linked to resource availability (Hodge et al. 2009) and therefore is also likely to have an influence on weight change during this period. We also include group size as an explanatory variable to control for any potential thermoregulatory effects of sleeping within a large or small group.

Weight change over the lactation period

The change in body weight over the lactation period was determined by calculating the average morning weight of each female during the pre- and the postlactation period and by calculating the difference. We do not compare subordinate groups with dominant lactators in this instance, as long-term weight change is likely to be influenced by behavioral differences associated with rank that are unlikely to influence weight change overnight. Dominant female weight change over the lactation period is also likely to be influenced by subsequent pregnancy, as the interbirth interval in meerkats is typically short (K. MacLeod, unpublished data).

We tested for differences between allonursing and non-allonursing control females in overall weight change by fitting weight change as an explanatory variable in GLMM, with allonursing status, group size, and rainfall specified as explanatory variables, with female identity as a random term to account for repeated measures. To account for the difference in age and prelactation mass between allonursing and non-allonursing subordinate females, and the potential that weight change may be linked to age-related growth, we include age as an explanatory variable in the model.

In a separate model, we investigated the effect of litter size on allonurse weight change by again fitting weight change as a response variable in a GLMM with litter size, group size, and average daily rainfall during the lactation period specified as continuous explanatory variables. We do not include litter size in previous models or include non-allonursing subordinate females in this model because, during the lactation period (i.e., before pup-provisioning begins), there is no reason to expect that the size of the litter in a group should have any influence on the weight change of non-allonursing subordinate females. Female and litter identity were included as random terms to control for repeat measures.

Behavioral changes during the prelactation, lactation, and postlactation periods

To compare the rates of behaviors of allonursing subordinate females with non-allonursing females, we selected a comparison control group: the oldest non-allonursing subordinate females in each group, with a minimum age of 1 year. Although a random selection of subordinate females across age groups would perhaps be preferable, these females were chosen for a number of reasons. First, for the purposes of creating a meaningful comparison group for allonursing subordinate females, we required females that did not differ significantly in age and body mass from allonurses, as these variables have been shown to influence contributions to cooperative behaviors (Clutton-Brock et al. 2002). In our selection, there were no significant differences between allonurses and controls in prelactation weight (Student's t-test: T 46 = 1.1, P = 0.28) or age (Mann–Whitney U-test: W 42 = 252.5, P = 0.56). Second, selecting females for comparison that were close in age and mass to allonurses also attempts to standardize the social environment of subordinate females, which is likely to influence behavior. The oldest females in a meerkat group are most likely to be evicted by the dominant female (Clutton-Brock et al. 2008), and to attempt to breed (Clutton-Brock et al. 2001), both factors known to influence allonursing probability (MacLeod et al. 2013). In our selection, the proportion of females in each group that had recently been evicted was comparable (37% of control females, 40% of allonurses). There was greater divergence in the proportion of females that had recently been, or were, pregnant (6% of control females, 32% of allonurses); however, due to the close physiological link between allonursing and pregnancy, this is an unavoidable discrepancy. Our final focal group included 20 allonurses and 28 control females.

Focal observations from the prelactation, lactation, and postlactation periods were extracted for each female corresponding to their own lactation or, in the case of subordinate control females, corresponding to the lactation of a female in their group. For each female, the total numbers of seconds dedicated to burrow renovation, raised guarding, resting, or foraging per period was calculated. The total observation time per period was also calculated, in seconds. We also classed pup-feeding and babysitting as cooperative, but as these only occur in the postlactation and lactation periods, respectively, we analyzed these separately and were not able to compare across periods. Pup feeds were measured in events (feeds), and investment in babysitting was measured in half-day sessions.

We tested the proportion of time each individual spent on each behavior of interest using binomial generalized linear models, which we fitted using the lme4 package in R (Bates et al. 2008). To investigate whether allonursing and control females differ in levels of investment in the 4 types of behavior over the 3 periods, models for each behavior type were constructed with period and allonursing status as categorical explanatory variables. These models also included an interaction term (allonursing status × period) to account for differences across time (except when looking at pup-feeding, which only occurs in the postlactation period, and babysitting, which only occurs in the lactation period). Environmental variation was accounted for in all models by including the average daily rainfall in each period (mls) and group size (number of adult individuals) as explanatory variables. These were also included in interactions terms with allonursing status to test for differences between allonursing and non-allonursing control females according to different environmental conditions. To control for social factors that might cause differences in behavior between allonursing and non-allonursing subordinate females, we include the following categorical explanatory variables: pregnancy status and eviction status. Pregnancy status was defined as follows: pregnant ("Y"), not pregnant ("N"), or recently having given birth, aborted, or lost a litter ("R"). If a female was first recorded as being pregnant less than 1 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 1 month before the birthdate of a litter, she was coded as "R" (recent birth/loss) at the time of that litter's birth. These distinctions have been shown to have important influences on allonursing likelihood and so may also influence behavioral differences (MacLeod et al. 2013). Eviction status was defined as whether females had recently been evicted from the group ("Y" = yes, "N" = no). Individual identity was included as a random term in all models to control for repeated measures. We also included individual-level random effects in all models to control for overdispersion. The significance of individual terms was determined by removing them from the model and testing the difference in model fit using Anovas. Final models after model selection are reported: where terms of interest did not appear in the final model, they are reported as P values obtained by removing them during the model selection process, with test statistics and degrees of freedom.

RESULTS

The costs of allonursing

Lactation status strongly predicted overnight weight loss during the period of lactation, with dominant lactators, as expected, losing much more weight overnight than either subordinate allonurses or control females (GLMM allonursing status $P < 0.001$; allonurses T 515 = 1.34, dominant lactators T 515 = 18.07). Rainfall was not included in the best model (χ2 1 = 1.67, $P = 0.20$) nor was group size (χ2 1 = 0.06, $P = 0.80$). Dominant mothers lost a mean of 58.97g ± 17.16 (N = 245) overnight, compared to subordinate allonurses and control females, which lost, on average, 31.87g ± 16.34 (N = 96) and 29.60g ± 11.24 (N = 179), respectively. Allonurse overnight weight loss during the period of allonursing did not significantly differ from that of control females (T-test: T 142.8 = 1.66, P = 0.09).

Allonursing females lost a mean of 1.43g ± 44.07 (N = 111) between the pre- and postlactation periods, a nonsignificant change in weight (paired T-test T 110 = 0.34, P = 0.73; Figure 1). In contrast, non-allonursing subordinates gained a mean of 20.07g ± 56.14 (N = 164) between the pre- and postlactation periods, a significant weight gain (paired T-test T 163 = −4.58, P < 0.001; Figure 1). Whether females allonursed or not was a significant predictor of how their weight changed over the lactation period (GLMM T 252, = −2.26, P ≤ 0.05). The strongest predictors of weight change over the lactation period were: female age at the start of the lactation period, with younger females gaining significantly more weight (GLMM T 252 = −4.16, P < 0.001) and rainfall, which increased weight gain (GLMM T 263 = 4.14, P < 0.001). Group size was not a significant predictor of weight change and did not appear in the final model (χ2 1 = 1.1, P = 0.75).

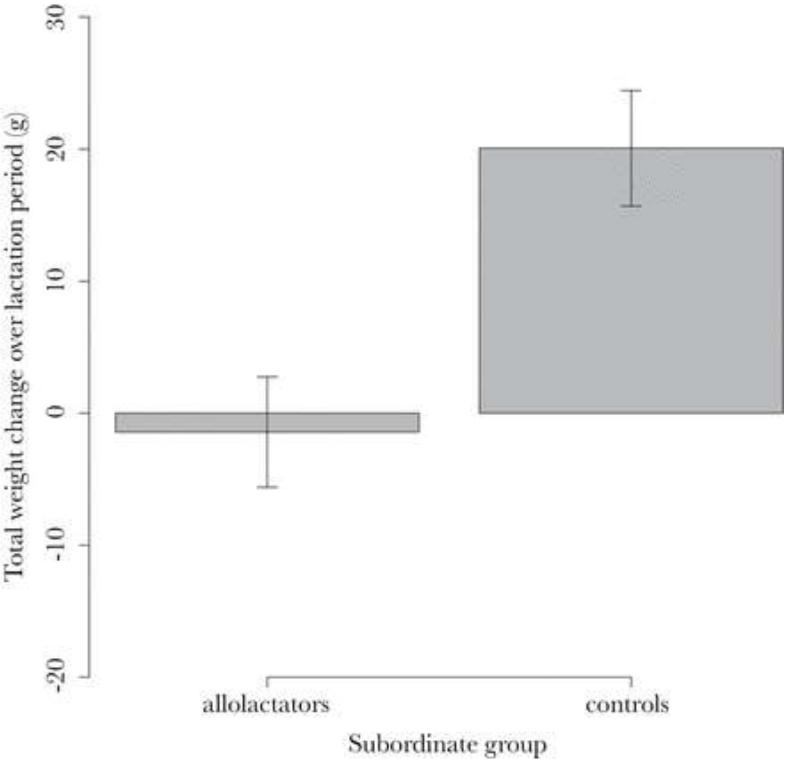

Figure 1 : Weight change (g) across the reproductive bout in allolactators and control females.

In allonursing females only, litter size did not influence weight change over the lactation period (did not appear in final model: χ2 1 = 0.67, P = 0.41). Group size also did not appear in the final model (χ2 1 = 0.09, P = 0.76). Rainfall, in this dataset, had a marginally nonsignificant positive effect on weight change (GLMM T 105 = 1.93, P = 0.06).

Behavioral changes during the prelactation, lactation, and postlactation periods

Allonurses spent more time foraging during the lactation period than in the pre- and postlactation periods, and relative to non-allonursing control females: an interaction term of allonursing status and period significantly predicted foraging rate (Figure 2a; Table 1, Foraging). Foraging rate was higher in the prelactation period and subsequently decreased in controls (Figure 2a). Eviction status (χ2 1 = 0.28, P = 0.60), pregnancy status (χ2 2 = 0.19, P = 0.91), rainfall (χ2 1 = 1.67, P = 0.20), and group size (χ2 1 = 1.5, P = 0.22) did not appear in the final model.

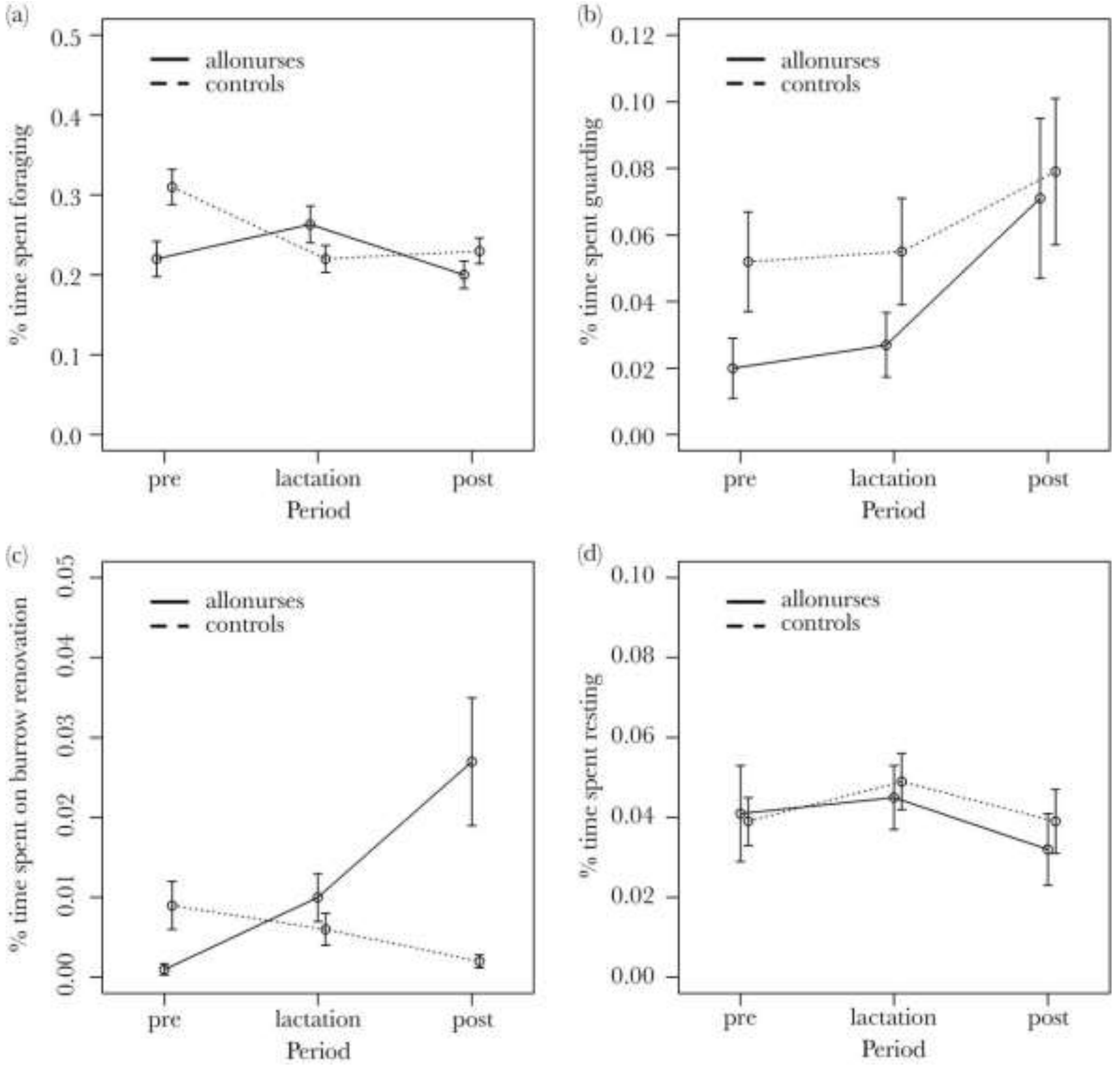

Figure 2 : Proportion of time (seconds/total seconds) spent foraging (a), raised guarding (b), renovating burrows (c), and resting (d) by subordinate allonurses and subordinate controls across the prelactation, lactation, and postlactation periods. Mean values are reported, and standard error bars are shown.

Table 1 : Results of binomial GLMMs investigating changes in investment in behaviors over the prelactation, lactation, and postlactation periods in allonursing subordinate females and non-allonursing control females

	Estimate	SE	*Z*	*P*	
(a) Foraging (DF = 118)	Intercept	−0.82	0.12	−6.88	
	Allonursing status × period				<0.01
	Allonurse: prelactation	0.00	0.22	3.81	
	Allonurse: lactation	0.83	0.24	1.73	
	Allonurse: postlactation	0.41			
(b) Raised guarding (DF = 118)	Intercept	−6.43	0.70	−9.16	
	Period				<0.01
	Prelactation	0.00	0.85	3.14	
	Lactation	2.68	0.92	2.49	

	Estimate	SE	Z	P	
	Postlactation	2.29			
	Rainfall	−0.67	0.24	−2.74	<0.01
	Pregnancy status				<0.05
	Not pregnant	0.00	2.00	0.92	
	Recently pregnant	1.84	1.08	−3.01	
	Pregnant	−3.25			
	Intercept	−8.78	1.09	−8.04	
	Allonursing status × period				<0.001
(c) Burrow renovation (DF = 115)	Allonurse: prelactation	0.00	1.53	1.81	
	Allonurse: lactation	2.77	1.62	4.12	
	Allonurse: postlactation	6.66			
	Allonursing status × rainfall				<0.001
	Allonurse	1.90	0.50	3.76	
	Group size	0.14	0.04	3.18	<0.001
	Intercept	−3.19	0.34	−9.49	
	Period				<0.05
(d) Resting (DF = 117)	Prelactation	0.00			
	Lactation	0.51	0.24	2.16	
	Postlactation	−0.03	0.25	−0.11	
	Allonursing status × rainfall				<0.05
	allonurse	−0.24	0.13	−1.91	
	Group size	−0.03	0.01	−1.91	0.05

Group size, rainfall, pregnancy status, and eviction status were included as explanatory variables. Female identity and individual-level random effect terms were included in all models as random terms. Best models after selection using Akaike Information Criterion (Akaike 1974) are reported. DF, degrees of freedom; SE, standard error.

The rate of raised guarding increased between the pre- and postlactation period in both allonurses and controls (Table 1, Raised guarding; Figure 2b). The 2 groups did not differ from each other in rates of raised guarding across periods (χ2 2 = 2.47, P = 0.29) or independent of period (χ2 1 = 0.15, P = 0.70); neither the interaction term allonursing status × period nor allonursing status alone appeared in the final model. Rainfall was associated with an overall decrease in raised guarding (Table 1, Raised guarding). Pregnant females invested significantly less time in raised guarding relative to nonpregnant females and those that had recently lost litters (Table 1, Raised guarding). Eviction status (χ2 1 = 0.10, P = 0.75) and group size (χ2 1 = 0.13, P = 0.72) did not appear in any final models.

Allonurses significantly increased their investment in burrow renovation over the 3 periods and relative to control females (Table 1, Burrow renovation; Figure 2c); in contrast, control females decreased investment in burrow renovation (Figure 2c). Females spent more time on burrow renovation in larger groups. Rainfall significantly positively influenced investment in burrow renovation in allonursing females only. Eviction status (χ2 1 = 2.70, P = 0.10) and pregnancy status did not appear in the final model (χ2 1 = 0.07, P = 0.96).

Both allonurses and control females rested more in the lactation period relative to the periods pre- and postlactation (Table 1, Resting; Figure 2d). Rainfall negatively influenced time spent resting in allonurses, and all females rested less in large groups (Table 1, Resting). Pregnancy (χ2 2 = 1.11, P = 0.57) and eviction status (χ2 1 = 1.70, P = 0.19) did not appear in the best model. An interaction term of allonursing status and period also did not appear in the final model (χ2 2 = 1.70, P = 0.43), indicating that allonurses did not differ from non-allonursing control females in resting rate across time.

In the postlactation period, allonurses did not differ from control females in frequency of pup-feeding; allonursing status did not appear in the final model (χ2 1 = 2.76, P = 0.09). Rainfall also did not appear in the final model (χ2 1 = 0.04, P = 0.85); nor did group size (χ2 1 = 2.22, P = 0.14) or pregnancy status (χ2 2 = 2.55, P = 0.28).

In the lactation period, allonursing females did not babysit pups significantly more than non-allonursing subordinate females: allonursing status did not appear in the final model (χ2 1 = 2.74, P = 0.10). Females that had recently been evicted were less likely to babysit during the lactation period (GLMM Z 56 = −2.01, P < 0.05). Rainfall did not influence babysitting rates (did not appear in the final model) (χ2 1 = 0.21, P = 0.65); nor did group size (χ2 1 = 0.37, P = 0.55) or pregnancy status (χ2 2 = 2.31, P = 0.31).

DISCUSSION

Contrary to predictions and indications from previous work (Scantlebury et al. 2002), our results show that allonursing subordinate females did not suffer reduced body mass over the period of allonursing and did not show increased overnight weight loss during the period of lactation relative to non-allonursing subordinate females. By contrast, non-allonursing subordinates gained weight during this time, probably because rainfall increases over the breeding season (Russell et al. 2002) and is linked to food availability (Hodge et al. 2009). If weight gain over the breeding bout is to be expected, as indicated by the weight gain by non-allonurses, then it is likely that allonursing females sustain some energetic costs through allonursing. The lack of significant weight change over the allonursing period, however, suggests that the long-term costs of this behavior are likely to be minimal. There are 2 possible explanations for this lack of evidence for a substantial cost of allonursing, as was predicted. First, allonursing simply may under some circumstances incur low costs, for example, when females have excess milk (Pusey and Packer 1994), and may be more likely to occur under these circumstances in the meerkat. Second, allonursing female meerkats may successfully mitigate the costs of allonursing through increased foraging during the allonursing period.

Allonursing may occur in meerkats when the energetic costs are low, in order to avoid long-term fitness costs. Subordinate female meerkats are most likely to allonurse when they have recently lost litters of their own (MacLeod et al. 2013); this is also the case in galagos (Galago senegalensis braccatus: Kessler and Nash 2010) and Northern Elephant seals (Mirounga angustirostris: Riedman and Le Bouef 1982), where allonursing following the loss of a neonate has been observed. Females that have recently lost litters are likely to have excess milk, reducing the costs of diverting this resource to nonoffspring (Packer et al. 1992). Allonursing in this case may be akin to “milk-dumping,” where females appear to readily give up milk not consumed by their own offspring, as in evening bats (Nycticeius humeralis: Wilkinson 1992) and grey seals (Halichoerus grypus: Beck et al. 2000). Allonursing where the costs are low has also been shown in lions (Panthera leo), where allonursing is thought to primarily have arisen as a low-cost by-product of communal living as a defense against infanticide (Pusey and Packer 1994). Female lions are more tolerant of nonoffspring nursing when they have small litters or when their own offspring are nearing weaning, both instances where they have excess milk. These results are in line with those of a recent comparative analysis of group-living mammals that showed that, where females live with kin and so are likely to gain some indirect benefits from allonursing, allonursing evolves where the costs are low, and not according to variation in the potential benefits to allonurses (i.e., where relatedness between females is very high) (MacLeod and Lukas 2014).

Alternatively, or additionally, allonursing female meerkats may successfully mitigate the energetic costs of allonursing by increasing their food intake. We show that allonurses spent more time foraging while they were lactating than control females, and that they significantly increased their rate of foraging during the lactation period relative to before and after allonursing. Other studies investigating the costs of lactation to mothers have found similar increases in foraging effort, suggesting that food intake is adaptively increased to meet the energetic demands of lactation (Gittleman and Thompson 1988; Bowen et al. 2001). For example, female saddle-back tamarins (Saguinus fuscicollis) increase time spent feeding during lactation (Goldizen 1987). Showing similar patterns, captive female cotton-top tamarins (Saguinus oedipus) increase their rate of feeding by up to 2 times the rate during pregnancy (Price 1992). Whether these increases in foraging effort offset the costs of lactation in terms of weight loss is unknown. Further work would be required to prove that this is the case in the meerkat, as our results tentatively suggest. For example, supplemental feeding of allonursing females followed by behavioral observation could determine whether the increase in foraging rate is in response to the energetic demands of allonursing; if this was the case, it might be expected that in food-supplemented females, foraging rate would not increase as it does in nonsupplemented allonurses.

Contrary to predictions, allonurses showed an increase in cooperative noncare behaviors (burrow maintenance and raised guarding) and did not reduce investment in babysitting during the allonursing period. Individual differences in contributions to cooperation have been shown to be highly repeatable (English et al. 2010) and levels of contributions to different behaviors are correlated (Clutton-Brock et al. 2003), so it is possible that allonurses increase contributions to guarding and burrow renovation while allonursing because they are relatively highly cooperative individuals. However, if allonurses were consistently more cooperative, they would be expected to have higher overall rates of cooperative behavior relative to non-allonursing subordinate females, and this was not the case. Instead, there may be no trade-off between allonursing and noncare cooperative behaviors as we predicted because the costs of raised guarding and burrow renovation are relatively low. As most guarding and bolt-hole renovation bouts last only a few minutes, costs incurred through energetic demand or lost foraging time are likely to be trivial, while the potential benefits of these antipredator behaviors are high (Clutton-Brock et al. 1999). Why allonurses do not reduce rates of babysitting is unclear as this behavior has been shown to carry high costs (Clutton-Brock et al. 1998). One possible explanation is that babysitting facilitates allonursing: allonurses may continue to babysit at high levels relative to predictions in order to allow pups to suckle during the day.

A further alternative is that increased investment in cooperative behaviors during and after the allonursing period serves a social function. The most frequent allonurses are subordinate females which have recently returned from a forced eviction from the group, or those which have recently lost a litter through abortion or infanticide (MacLeod et al. 2013). High contributions to cooperative behaviors may be a way of ensuring renewed access to or tolerance within the social group in accordance with the “pay-to-stay” hypothesis (Gaston 1978). Helpers temporarily separated from their social group subsequently increase helping effort in the cooperatively breeding cichlid species

N. pulcher, resulting in a decrease in aggression toward them (Balshine-Earn et al. 1998; Bergmüller and Taborsky 2005). The increase in cooperative behavior including allonursing in allonursing females may similarly increase the tolerance of dominant female meerkats to returning subordinates: behavioral assays would be required to confirm a decrease in aggression. However, as there is no evidence that dominant female meerkats use aggression to promote helping (Santema and Clutton-Brock 2012), this may be unlikely in this species.

Allonursing female meerkats do not sustain weight loss as a result of allonursing, meaning that the fitness costs of this behavior are likely to be low. Whether this low cost of allonursing is due to females having excess milk, or successfully mitigating the costs of allonursing, remains unclear and would benefit from further study. In either case, the maintenance of body condition during allonursing is significant in understanding the evolutionary history of this behavior in meerkats. In this species, body mass is strongly associated with increased survival, fecundity, and the likelihood of dominance acquisition (Clutton-Brock et al. 2001; Russell et al. 2003a; Hodge et al. 2008) and is therefore an important metric of potential reproductive fitness. Low or mitigated costs of allonursing therefore have reduced implications for individual fitness. As relatedness in meerkat groups is high (MacLeod et al. 2013) and indirect benefits are therefore likely, the benefits of allonursing are likely to vastly outweigh the low costs, especially if allonursing also provides social benefits. These results are therefore helpful in understanding how this behavior is maintained in this species. From this analysis alone, however, we cannot exclude other potential hypotheses for allonursing in this species; further research on the benefits that allonurses may accrue would help to illuminate the adaptive nature of this behavior.

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