



Meerkat helpers increase sentinel behaviour and bipedal vigilance in the presence of pups

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ARTICLE INFO

Article history:

Received 13 September 2012
Initial acceptance 22 November 2012
Final acceptance 20 December 2012
Available online 5 February 2013
MS. number: 12-00707R

Keywords:

cooperative breeding
helping
meerkat
sentinel
Suricata suricatta
vigilance

Helpers in cooperatively breeding species may assist in a number of cooperative activities, such as nest building, incubating, babysitting and feeding of offspring. In addition, individuals may engage in sentinel behaviour and other forms of vigilance, which benefits other group members not only by reducing the risk of predation, but also by allowing them to reduce their own vigilance. It remains unclear, however, whether these vigilance behaviours are selfish, and the benefits to other group members simply an unselected by-product, or whether they are forms of cooperation, and the benefits to group members a selective force favouring the behaviour. In meerkats, *Suricata suricatta*, both female and male helpers were more likely to perform sentinel behaviour after dependent pups had started joining the group on foraging trips. In addition, female helpers performed more bipedal vigilance and found less food when pups were in the group. These results suggest that sentinel behaviour and bipedal vigilance represent forms of cooperation in meerkats.

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Cooperative breeders, in which nonbreeding helpers assist in rearing offspring born to breeders, have attracted much research interest and have served as a model system to study processes underlying cooperation at large (Bergmüller et al. 2007). Helpers in cooperatively breeding species assist in a number of cooperative activities, such as nest building, incubating, babysitting and feeding of offspring (e.g. Stacey & Koenig 1990; Koenig & Dickinson 2004). In addition, group members may engage in vigilance behaviours, such as sentinel behaviour (Rasa 1986; Clutton-Brock et al. 1999; Wright et al. 2001a). Such vigilance behaviours benefit other group members not only by reducing the risk of predation, but also by allowing them to reduce their own vigilance and, hence, increase their foraging efficiency (Manser 1999; Krause & Ruxton 2002; Hollén et al. 2008; Bell et al. 2009; Ridley et al. 2010). Although it is clear that individuals can benefit from vigilance behaviour by other group members, it remains unclear whether these benefits are simply an unselected by-product or a selective force favouring these behaviours.

Vigilance behaviours in cooperative breeders, in particular sentinel behaviour, were traditionally thought to be favoured by the benefits provided to other group members through kin selection or reciprocity (e.g. Rasa 1989). However, a model developed

by Bednekoff (1997) showed that sentinel behaviour may, in fact, simply be an individual's optimal behaviour if it is satiated and no other individual is already on sentinel duty. Subsequent empirical studies showed that sentinel behaviour is indeed often dependent on an individual's nutritional state, and that supplementary feeding of individuals increases their sentinel behaviour, leading to the conclusion that sentinel behaviour may indeed simply be explained by immediate selfish benefits (Clutton-Brock et al. 1999; Wright et al. 2001a, b, c; Bednekoff & Woolfenden 2003). However, contributions to many cooperative activities are condition dependent and supplementary feeding leads to increases in many cooperative behaviours (Boland et al. 1997; Wright & Dingemanse 1999; Clutton-Brock et al. 2000, 2001, 2002; Russell et al. 2003). Thus, while these findings are consistent with Bednekoff's model, they do not exclude the possibility that benefits to other group members may reinforce the expression of sentinel behaviour. Indeed, recent work on cooperative breeders shows that sentinels may be more susceptible to predation than foragers, which is in direct contrast with the predictions of Bednekoff's model (Ridley et al. 2013). As yet, it is unclear whether sentinel behaviour and other vigilance behaviours in cooperative breeders are favoured by the benefits they provide to other group members, and more direct tests are needed.

Meerkats, *Suricata suricatta*, are cooperative breeders that live in groups consisting of a dominant breeding pair and up to 40 subordinate helpers of both sexes who do not normally breed (Griffin

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et al. 2003). They forage for up to 8 h per day in the open, during which group members engage in two distinct forms of vigilance behaviour (Clutton-Brock et al. 1999). First, individuals occasionally cease foraging and climb to an elevated position to scan the area, an activity referred to as 'sentinel behaviour'. Individuals are on sentinel duty for an average of 0.2 times/h and bouts typically last a few minutes, but variation between individuals and groups can be large (Clutton-Brock et al. 1999). Second, individuals frequently interrupt foraging for short periods to adopt a bipedal position and glance around to scan the environment, an activity we refer to as 'bipedal vigilance'. Bipedal vigilance is typically performed once every couple of minutes and bouts last a few seconds (Clutton-Brock et al. 1999; P. Santema, unpublished data). Meerkats on sentinel or bipedal vigilance give acoustically distinct calls that allow other group members to reduce their own vigilance behaviour (Manser 1999; Townsend et al. 2011). Upon detecting a predator, they warn the rest of the group using a system of several different alarm calls (Manser 1999, 2001). Following birth of a litter, pups initially remain behind at the breeding den when the group leaves the burrow to forage for the day. At about 30 days of age, the pups start accompanying the group on foraging trips, but remain nutritionally dependent on adults until approximately 90 days of age (Clutton-Brock et al. 2002, 2003).

We investigated whether meerkat helpers increase their sentinel behaviour and bipedal vigilance when dependent pups start joining the group on foraging trips, compared to the preceding period when pups remain behind at the breeding burrow. If sentinel behaviour and bipedal vigilance are selfish, we expected that the presence of pups in the group would not affect the expression of these behaviours. However, if sentinel behaviour and bipedal vigilance are forms of cooperation, we expected that helpers would increase the expression of these behaviours when dependent offspring are present in the group. To test for potential costs associated with changes in sentinel behaviour and bipedal vigilance, we also examined changes in foraging time and amount of food found. Second, we focused on the period after the pups had joined the group on foraging trips to examine whether the proximity of pups is associated with changes in bipedal vigilance, time spent foraging and amount of food found.

METHODS

Study Site and Population

The study was conducted in the southern Kalahari Desert, South Africa (26°58'S, 21°49'E) with permission from the Northern Cape Conservation Authority. All meerkats in the study were habituated to close observation (<1 m) and could be identified by a unique pattern of dye marks on their fur, which was applied with a paint brush while individuals were resting without the need to disturb or capture them. Dominance status of males and females was readily identified as subordinate helpers are behaviourally submissive to dominants (O'Riain et al. 2000). Groups were visited at least once every 3 days and birth dates were identified from dramatic weight loss following a period of gradual weight gain, as well as the onset of babysitting behaviour. The age of almost all individuals was therefore known to within a few days. Our study focused on individuals of at least 6 months of age, as individuals below this age still invest heavily in growth and their contributions to cooperative activities are typically low (Clutton-Brock et al. 2002).

Observation Protocol

Between October 2011 and March 2012, focal observations (Altmann 1974) were performed on 40 female helpers and 49 male helpers from 11 different groups. Two 30 min observations,

separated by at least 30 min, were performed on each individual shortly before the pups started joining the group on foraging trips (pup age 15–30 days). Another two 30 min observations, again separated by at least 30 min, were performed on each individual shortly after the pups had started joining the group on foraging trips (pup age 31–45 days). All observations on an individual were performed during the same breeding cycle, such that the time between the two sets of observation was never greater than 30 days (mean = 17 days). Variation caused by seasonal factors, such as weather conditions or daylength, or demographic factors, such as group size, was therefore minimal. During each observation, the number of times the individual performed bipedal vigilance, the time spent in close proximity (<2 m) to a pup, the time spent foraging and the number of food items found were recorded. Following previous studies, each food item found was categorized as tiny, small, medium or large (Thornton 2008). The total amount of food found per observation was then estimated using the average mass of the food items in each size category (tiny = 0.05 g, small = 0.11 g, medium = 0.58 g, large = 2.86 g; Thornton 2008). Behavioural data were entered directly onto a handheld Psion organizer (Psion Teklogix Inc., Ontario, Canada), programmed as a data logger that allows recording of behaviours to the nearest second (Santema & Clutton-Brock 2012). One group was visited each day and observations started after the group had left the burrow to forage and continued until the group became inactive at midday. Depending on when the group became inactive, one to six observations were performed per session. Observations were paused if foraging was interrupted for more than 1 min (e.g. by alarm calls) and continued when foraging had been resumed by at least 50% of the group (Santema & Clutton-Brock 2012).

Because the frequency of sentinel behaviour was comparatively low, and, unlike the other behaviours of interest, could easily be monitored for all individuals in the group simultaneously, all instances of sentinel behaviour by every group member were recorded during each observation session. An individual was considered to be on sentinel duty when it was scanning for at least 10 s from at least 10 cm above ground level. The occurrence of sentinel behaviour was recorded continuously over the duration of the observation session, such that recording periods varied from 30 min to 180 min, depending on how many focal observations were performed during that session. In total, this resulted in an average of 19 ± 3 SE observation hours on 177 helpers from 11 different groups, during which 459 instances of sentinel behaviour were recorded.

Statistical Analyses

All analyses were performed using generalized linear mixed models (GLMM) with the lme4 package (Bates et al. 2011) in R 2.13 (R Development Core Team 2011). Individual identity and group identity were included in all models as random terms. Because of the different life histories of females and males, the factors affecting contributions to various activities in meerkats are often sex-specific (Clutton-Brock et al. 2002). Therefore, our analyses were performed for males and females separately in order to increase the ease of interpretation of the results. Square-root transformation of the response variable was applied when this was required to achieve normality of the model residuals. Besides the variables of interest, all initial models included group size (number of individuals > 6 months) and average wind speed (recorded on site) on the day of data collection to control for the potentially confounding effects of these factors. Models were refined using backwards stepwise deletion; model terms were removed in order of increasing test statistic value if likelihood ratio tests indicated that they did not explain significant variation. This process was repeated until the minimal adequate model was obtained with only variables that

Table 1
Relation between presence of pups and sentinel behaviour

	Fixed factor	Estimate	SE	Test statistic	P
Female helper	Intercept	−1.887	0.292		
	Presence	1.150	0.292	3.932	<0.001
	Duration	0.425	0.138	3.085	0.002
	Group size	−0.047	0.029	−1.626	0.175
	Wind speed	−0.215	0.227	−0.945	0.343
Male helper	Intercept	−2.145	0.422		
	Presence	0.713	0.190	3.747	<0.001
	Duration	0.799	0.104	7.687	<0.001
	Group size	−0.025	0.038	−0.672	0.513
	Wind speed	0.037	0.152	0.244	0.081

Table represents summaries of the GLMMs examining the relation between presence of pups in the foraging group (yes/no) and whether or not sentinel behaviour was performed during an observation for female helpers ($N = 761$ observations, 71 individuals, 11 groups) and male helpers ($N = 1207$ observations, 103 individuals, 11 groups). Fixed factors represented in bold were included in the final model.

explained a significant amount of variation ($P < 0.05$). The significance of the terms that were included in the minimal model was examined using a log-likelihood test, by comparing the minimal model to the model in which the term had been removed. The level of nonsignificance of each dropped term was examined by putting the term back into the minimal model and comparing this model to the minimal model using a log-likelihood test (Crawley 2007).

To examine how the presence of pups in the foraging group (henceforth 'presence') was associated with sentinel behaviour, each individual was classified for each observation period as either 0 (did not perform sentinel behaviour) or 1 (did perform sentinel behaviour). We adopted this binomial approach as the number of observations in which an individual did not perform any sentinel behaviour was large (78%) whereas the number of observations in which an individual was on sentinel more than once was small (12%), and thus the data did not adhere to assumptions of Gaussian distribution. Whether or not an individual performed sentinel behaviour was used as the response variable in GLMMs fitted to a binomial error structure. Presence, duration of the observation period, group size and wind speed were included as fixed effects.

Table 2
Relations between the presence of pups and bipedal vigilance, time spent foraging and amount of food found

	Fixed factor	Estimate	SE	Test statistic	P
Female helper	Bipedal vigilance	Intercept	2.416	0.077	
		Presence	0.199	0.047	4.189
		Group size	−0.003	0.009	−0.349
		Wind speed	−0.018	0.046	−0.380
	Foraging time	Intercept	925.94	29.33	
		Presence	−65.36	28.24	−2.315
		Group size	−5.104	3.328	−1.534
		Wind speed	−10.83	23.26	−0.466
	Biomass found (sqrt)	Intercept	0.086	0.051	
		Presence	−0.150	0.060	−2.499
Male helper	Bipedal vigilance	Group size	−0.005	0.006	−0.802
		Wind speed	−0.003	0.047	−0.059
		Intercept	2.517	0.093	
		Wind speed	−0.121	0.036	−3.341
	Foraging time	Presence	0.037	0.044	0.839
		Group size	−0.005	0.006	−0.716
		Intercept	939.01	18.99	
		Presence	−14.65	25.27	−0.58
	Biomass found (sqrt)	Group size	−3.414	2.241	−1.524
		Wind speed	−12.74	19.26	−0.661
		Intercept	1.141	0.042	
		Presence	−0.022	0.058	−0.369
		Group size	−0.003	0.005	−0.555
		Wind speed	0.027	0.042	0.630
					0.514

Table represents summaries of the GLMMs examining relations between the presence of pups in the foraging group (yes/no) and the number of times performing bipedal vigilance, time spent foraging (min) and amount of food found (g) per 30 min observation for female helpers ($N = 160$ observations, 40 individuals, 11 groups) and male helpers ($N = 196$ observations, 49 individuals, 10 groups). Fixed factors represented in bold were included in the final model.

To examine how the presence of pups was associated with bipedal vigilance, foraging time and amount of food found, GLMMs were constructed with the behaviour of interest included as the response variable and presence, group size and wind speed as fixed effects. The models examining bipedal vigilance were fitted to a Poisson error distribution whereas the models examining foraging time and amount of food found (square-root transformed) were fitted to a normal error distribution.

To examine how the proximity of pups was associated with bipedal vigilance, foraging time and amount of food found, analyses were restricted to observations carried out after the pups had started foraging with the group. For each observation, the amount of time in close proximity (<2 m) of a pup and the amount of time not in close proximity of a pup were obtained, as well as the number of times performing bipedal vigilance, foraging time and amount of food found for each of these periods. For both the period close to a pup and the period not close to a pup, we then calculated the frequency of bipedal vigilance (times/30 min) the proportion of time spent foraging and amount of food found (g/30 min). GLMMs were then constructed with the behaviour of interest included as the response variable, and whether or not a pup was in close proximity, group size and wind speed as fixed effects. All models were fitted to a normal error distribution.

To examine whether females and males differed in the proportion of time spent in close proximity to pups, analyses were again restricted to observations carried out after the pups had started foraging with the group. A GLMM was then constructed with the number of seconds spent close to a pup (square-root transformed) as a response variable fitted to a normal error distribution, and sex, group size and wind speed as fixed effects.

RESULTS

Presence of Pups

Both female and male helpers were more likely to perform sentinel behaviour after the pups had joined the group on foraging

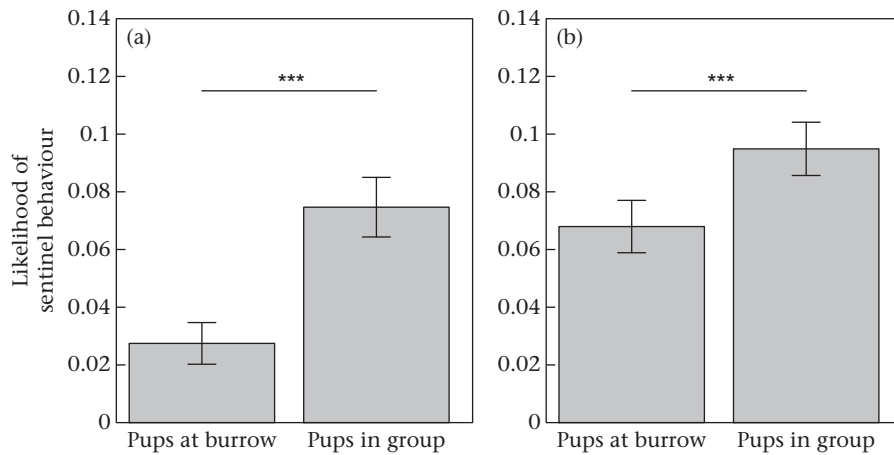


Figure 1. Relation between whether or not pups are present in the foraging group and the likelihood of performing sentinel behaviour for (a) female and (b) male helpers. Bars represent mean per 30 min observation \pm SE. *** $P = 0.001$.

trips (Table 1, Fig. 1). In addition, female helpers performed more bipedal vigilance after the pups had joined the group on foraging trips, but there was no change for males (Table 2, Fig. 2a, b). Female helpers spent less time foraging and found less food after the pups had joined the group on foraging trips (Table 2, Fig. 2c, e), whereas there was no change for males in either the time spent foraging or amount of food found (Table 2, Fig. 2d, f).

Proximity of Pups

Both female and male helpers performed more bipedal vigilance when pups were in close proximity (Table 3, Fig. 3a, b). In addition,

both male and female helpers spent less time foraging when in close proximity to pups (Table 3, Fig. 3c, d). Finally, both female and male helpers found less food when in close proximity to pups (Table 3, Fig. 3e, f). When pups were present in the group, female helpers spent more time in close proximity (<2 m) to pups than male helpers (Table 4, Fig. 4).

DISCUSSION

Collective antipredator vigilance is an important benefit of living in cooperative groups (Rasa 1989; Clutton-Brock et al. 1999; Hollén et al. 2008; Bell et al. 2009; Ridley et al. 2010). It remains

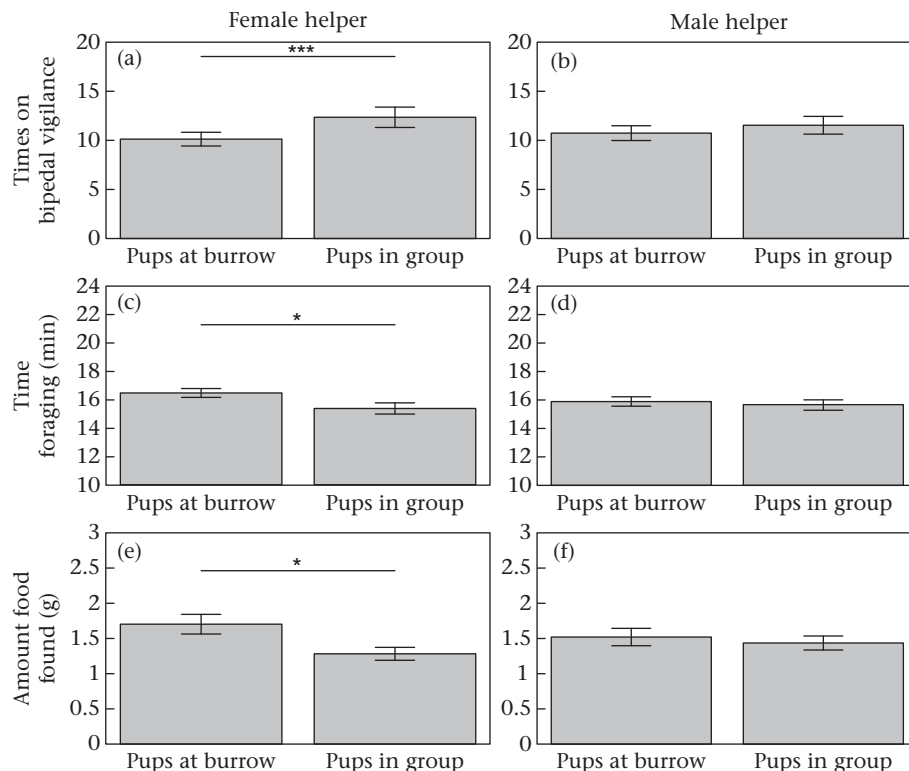


Figure 2. Relation between whether or not pups are present in the foraging group and (a, b) number of times performing bipedal vigilance, (c, d) time spent foraging and (e, f) amount of food found for female and male helpers. Bars represent mean per 30 min observation \pm SE. * $P = 0.05$; *** $P = 0.001$.

Table 3

Relations between proximity to pups and bipedal vigilance, time spent foraging and amount of food found

		Fixed factor	Estimate	SE	Test statistic	P
Female helper	Bipedal vigilance	Intercept	17.036	3.540		
		Proximity	6.193	2.212	2.800	0.006
		Wind speed	−3.631	1.843	−1.970	0.049
	Foraging time	Group size	0.097	0.189	0.515	0.611
		Intercept	0.524	0.030	17.540	
		Proximity	−0.138	0.024	−5.730	<0.001
	Biomass found (sqrt)	Wind speed	−0.005	0.003	−1.345	0.173
		Group size	−0.016	0.028	−0.584	0.575
		Intercept	1.122	0.072	15.532	
		Proximity	−0.430	0.094	−4.569	<0.001
		Group size	−0.013	0.007	−1.928	0.052
		Wind speed	0.050	0.078	0.639	0.565
Male helper	Bipedal vigilance	Intercept	9.526	1.618		
		Proximity	5.871	1.543	3.804	<0.001
		Group size	−0.051	0.180	−0.285	0.786
	Foraging time	Wind speed	−1.084	1.792	−0.605	0.543
		Intercept	0.666	0.057	11.658	
		Proximity	−0.105	0.023	−4.605	<0.001
	Biomass found (sqrt)	Group size	−0.007	0.003	−2.561	0.020
		Wind speed	−0.011	0.026	−0.423	0.687
		Intercept	1.090	0.069	15.863	
		Proximity	−0.435	0.085	−5.135	<0.001
		Group size	−0.006	0.007	−0.848	0.393
		Wind speed	−0.017	0.073	−0.234	0.823

Table represents summaries of the GLMMs examining relations between whether or not pups are in close proximity (<2 m) and the frequency of bipedal vigilance (times/30 min), proportion of time spent foraging and amount of food found (g/30 min) for female helpers ($N = 80$ observations, 40 individuals, 11 groups) and male helpers ($N = 98$ observations, 49 individuals, 10 groups). Fixed factors represented in bold were included in the final model.

unclear, however, whether sentinel behaviour and other vigilance behaviours in cooperative breeders are selfish behaviours, and the benefits to other group members merely an unselected by-product, or whether they represent forms of cooperation, and the benefits to other group member favour its expression. We have shown that both female and male meerkat helpers were more likely to perform sentinel behaviour after pups had joined the group on foraging trips. In addition, female helpers performed bipedal vigilance more frequently, spent less time foraging and found less food when pups were in the group. These results suggest that the survival benefit to pups promotes the expression of sentinel behaviour and bipedal vigilance in meerkat helpers, and that these behaviours thus represent forms of cooperation.

Both female and male helpers performed bipedal vigilance more frequently when they were in close proximity (<2 m) to a pup. In addition, both female and male helpers spent less time foraging and found less food when in close proximity to a pup. However, when pups were in the group, female helpers spent more time close to them than male helpers. Therefore, the fact that females, but not males, showed a significant increase in bipedal vigilance and found less food after pups joined the group on foraging trips seems to be because female helpers spent more time close to pups rather than because they were more responsive to them.

Whereas female helpers increased levels of bipedal vigilance, spent less time foraging and found less food when pups were present in the group, males did not show such changes. One explanation for this difference may be that female helpers gain more from the survival of offspring than male helpers. As females are the philopatric sex in meerkats, they are likely to benefit from increased group size (Kokko et al. 2001), as group size is associated with increased survival and reproduction in meerkats (Clutton-Brock et al. 2002). Alternatively, this difference may be driven by sex differences in the costs of bipedal vigilance. For instance, as males often visit neighbouring groups during the breeding season to prospect for mating opportunities (Young et al. 2005), they may not be able to afford to reduce their food intake and to perform more bipedal vigilance, as this may be

traded off against prospecting behaviour. As females never leave their group voluntarily, such a trade-off is unlikely to be present in females.

Because of the correlational nature of the data, it is not possible to infer a causal relation between the presence of pups in the group and the increase in sentinel behaviour and bipedal vigilance by helpers. However, as we performed all observations on an individual in the same breeding cycle, variation between observations in environmental and demographic factors was minimal. Nevertheless, the presence of pups in the group may have been associated with factors that we could not control for, which could have contributed to an increase in sentinel behaviour and bipedal vigilance. For instance, if the presence of pups attracts predators to the group, an increase in sentinel behaviour and bipedal vigilance could also result from an increase in predation risk (Haff & Magrath 2011). Future experimental work may further illuminate the factors underlying variation in sentinel behaviour and bipedal vigilance in meerkats.

In summary, we have shown that both female and male helpers were more likely to perform sentinel behaviour when pups were present in the group. In addition, female helpers performed more bipedal vigilance, spent less time foraging and found less food when pups were in the group. These results suggest that the benefits to other group members favour the expression of sentinel

Table 4

Relation between sex and the amount of time in close proximity to pups

Fixed factor	Estimate	SE	Test statistic	P
Intercept	4.009	0.461		
Sex	−0.467	0.226	−2.062	0.046
Group size	−0.079	0.022	−3.571	<0.001
Wind speed	0.242	0.183	1.324	0.169

Table represents summaries of the GLMM examining the relation between sex and the amount of time (min) spent in close proximity (<2 m) to a pup per 30 min observation ($N = 178$ observations, 89 individuals, 11 groups). Fixed factors represented in bold were included in the final model.

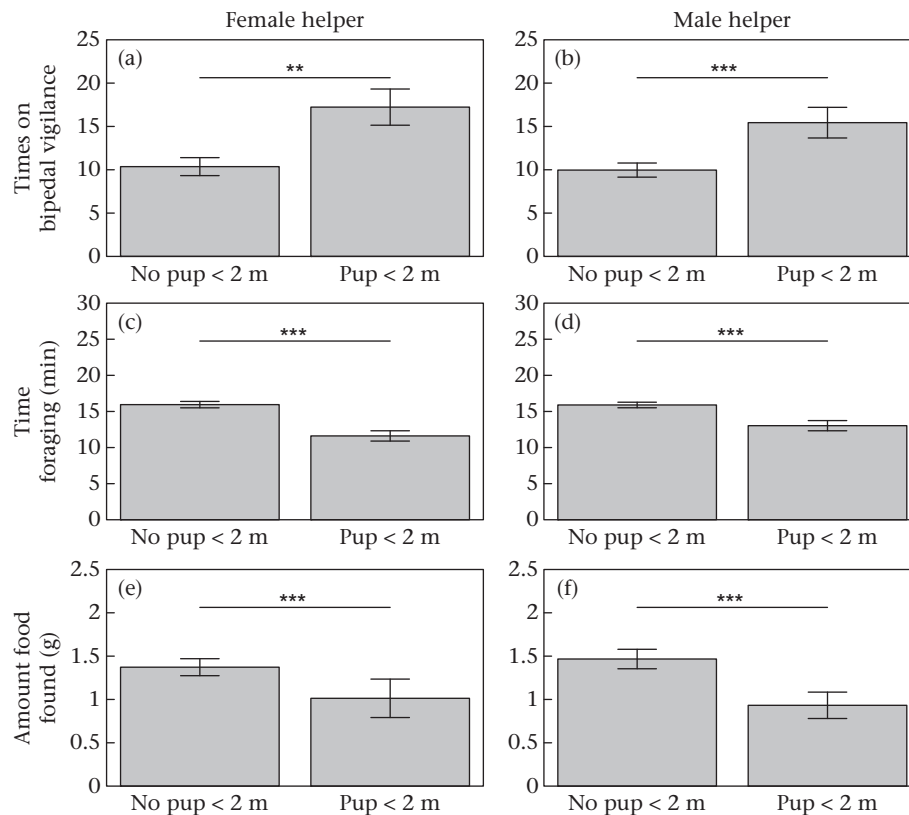


Figure 3. Relation between whether or not pups are in close proximity (<2 m) and (a, b) number of times on guard, (c, d) time spent foraging and (e, f) foraging success for female and male helpers. Bars represent means per 30 min \pm SE. ** $P = 0.01$; *** $P = 0.001$.

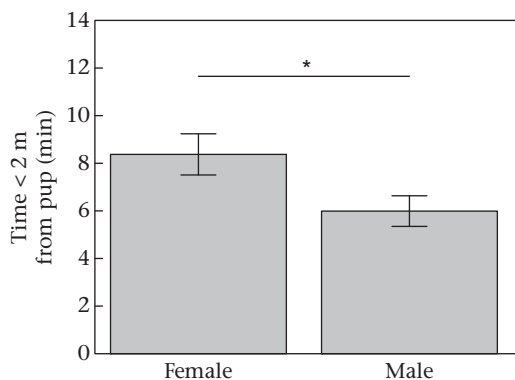


Figure 4. The amount of time spent in close proximity (<2 m) to a pup for female and male helpers. Bars represent mean per 30 min observation \pm SE. * $P = 0.05$.

behaviour and bipedal vigilance, thus classifying it as cooperation (West et al. 2007).

Acknowledgments

We are grateful to the Kotze family and other neighbouring farmers of the Kuruman River Reserve for allowing us to work on their land and to the Northern Cape Conservation Authority for granting permission to conduct research on meerkats in the Kalahari. We are indebted to Zachary Teitel and all meerkat project volunteers for invaluable help with the field work, to Marta Manser for support and advice on data collection, to Jamie Samson and Nathan Thavarajah for logistical support, and to Dieter Lukas, Elise

Huchard, Marta Manser, Markus Zöttl, and two anonymous referees for valuable comments on the manuscript. This study was funded by a research studentship from the Biotechnology and Biological Sciences Research Council to P.S. Additional financial support was provided by Cambridge European Trust, Balfour Fund and Prins Bernhard Cultuurfonds.

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