

Meerkats (*Suricata suricatta*) fail to prosocially donate food in an experimental set-up

Federica Amici^{1,2,3} · Montserrat Colell Mimó⁴ · Christoph von Borell⁵ · Nereida Bueno-Guerra^{4,6,7} 

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Abstract Although humans are usually believed to be prosocial, the evolutionary origins of prosociality are largely debated. One hypothesis is that cooperative breeding has been one major precursor to the emergence of prosociality. In vertebrates, however, experimental evidence of prosociality has been mainly gathered in non-human primates. In this study, we tested the cooperative breeding hypothesis in cooperative breeding meerkats (*Suricata suricatta*). In particular, we tested whether meerkats take

into account partners' benefits when distributing food rewards. Nine individuals were presented with two platforms baited with different food distributions (providing food to themselves, to a partner or both). In all conditions, the decision to operate the apparatus was based on the presence of food on the subject's side, and not on the possible benefits to partners. Despite being cooperative breeders, meerkats in this study failed to be prosocial, suggesting that prosociality in this species may be limited to specific contexts.

Christoph von Borell and Nereida Bueno-Guerra have contributed equally to this work.

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✉ Nereida Bueno-Guerra
nereidabuenoguerra@gmail.com

¹ Junior Research Group “Primate Kin Selection”, Institute of Biology, Faculty of Bioscience, Pharmacy and Psychology, University of Leipzig, Leipzig, Germany

² Department of Primatology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

³ Department of Developmental and Comparative Psychology, Institute of Psychology, University of Bern, Bern, Switzerland

⁴ Department of Clinical Psychology and Psychobiology, University of Barcelona, Barcelona, Spain

⁵ Institute of Psychology, Biological Personality Psychology, University of Göttingen, Göttingen, Germany

⁶ Department of Comparative and Developmental Psychology, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

⁷ Department of Psychology, Comillas Pontifical University, Madrid, Spain

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Introduction

Prosociality has been defined as any behaviour performed to alleviate others' needs or improve their welfare, without the actor necessarily incurring extra costs to provide these benefits (Cronin 2012). Through evolution, prosocial behaviours might have led to the emergence of cooperation, providing individuals with the psychological predisposition to be concerned for the welfare of others (e.g. Falk et al. 2003; Henrich et al. 2005; see Amici 2015, for a review). Although primates, for instance, appear to help others to obtain objects in both mutualistic and altruistic settings (e.g. chimpanzees, *Pan troglodytes*: Warneken and Tomasello 2006; Warneken et al. 2007; Yamamoto et al. 2012; but see Tennie et al. 2016), it is more controversial whether they prosocially donate food to others (for negative evidence, e.g. great apes, capuchin monkeys, *Sapajus apella*, and spider monkeys, *Ateles geoffroyi*: Amici et al. 2014; chimpanzees, *Pan troglodytes*: Jensen et al. 2006; Silk et al. 2005; Vonk et al. 2008; bonobos, *Pan paniscus*:

Tan et al. 2015; long-tailed macaques, *Macaca fascicularis*: Sterck et al. 2015; for positive evidence, e.g. capuchin monkeys: Lakshminarayanan and Santos 2008; Takimoto et al. 2010; for reviews, see Cronin 2012; Marshall-Pescini et al. 2016). In these studies, individuals typically choose between two trays, only one of which (also) provides food to the partner. Under controlled laboratory conditions, most primates are reliably indifferent to the welfare of others, even when they would incur no extra costs for donating food (e.g. Amici et al. 2014; Jensen et al. 2006; Silk et al. 2005; Vonk et al. 2008). These results may not be surprising: although some primates occasionally cooperate to obtain food (e.g. Boesch 1994, 2002), the largest majority of resources are gathered individually, so that foraging is overall a highly competitive activity (Van Schaik and Janson 1988; Isbell 1991) and prosociality in an active food distribution context may be especially demanding.

An important exception, however, might encompass cooperative breeders. Although the evolutionary processes that have favoured prosocial behaviour in humans may differ from those of other taxa (see Lukas and Clutton-Brock 2012; Silk and House 2016), all cooperative breeders may be especially motivated and psychologically predisposed to behave prosocially (Burkart et al. 2007, 2009). Common marmosets (*Callithrix jacchus*) and cotton-top tamarins (*Saguinus oedipus*) prosocially give food to partners (Burkart et al. 2007; Cronin et al. 2010), also in non-dyadic contexts (Burkart and van Schaik 2013). Across 15 primate species, including humans, prosociality has been proposed to be evolutionary linked to the emergence of extensive allo-maternal care (Burkart et al. 2014). However, two studies have failed to provide evidence of prosociality in cotton-top tamarins (Stevens 2010; Cronin et al. 2010). Moreover, under natural conditions cooperative breeders donate food almost exclusively to dependent pups (e.g. Izawa 1978; Rapaport and Ruiz-Miranda 2006), and adults' contribution largely varies depending on adults' physical condition and pups' signals (e.g. Heinsohn and Legge 1999; Clutton-Brock et al. 2001). Finally, the link between cooperative breeding and prosociality in a food context has only been tested in primates, and it is therefore still unknown whether it may also be valid across other taxa (see Thornton and McAuliffe 2015; Burkart and van Schaik 2016).

In this study, we experimentally tested prosociality in meerkats (*Suricata suricatta*), a cooperatively breeding carnivore (Clutton-Brock et al. 1999). Meerkats typically live in extended family groups in which the dominant breeding pair produces the majority of pups (Griffin et al. 2003). The other group members provide care for the dominants' offspring, babysitting pups (Clutton-Brock et al. 1998), feeding and keeping them safe (Brotherton

2001). Adults also contribute to other communal behaviours, including guarding against predators (Clutton-Brock et al. 1999), mobbing (Graw and Manser 2007) and excavating common burrows (Manser and Bell 2004). However, meerkats are not cooperative foragers, and food sharing in adults is rather rare (Clutton-Brock and Manser 2006). Pups remain at the sleeping burrow with a babysitter for their first month (Kunc et al. 2007) and in the following two months start foraging with the group, although they are largely dependent on the food donated by other group members (e.g. Brotherton 2001). Given these facts, meerkats are considered “a model species” to investigate prosocial behaviours (Madden and Clutton-Brock 2011), and we therefore predicted that they would be prosocial to each other also in an experimental set-up involving distribution of food resources.

Methods

Subjects

We tested a group of 12 meerkats at the Leipzig Zoo in Leipzig, Germany, including seven males and five females born in captivity (i.e. five juveniles and seven adults; mean age: 41 months, ranging from 5 to 126 months). No pups were in the group at the time of testing, although adults had contributed to infant care in previous litters. All subjects were housed together in a social group, in an enclosure with a larger outdoor area and an indoor area (circa 2×2 m). Testing was conducted in the indoor area, which subjects were free to access and leave during testing. Subjects had never been experimentally tested before, were never deprived of food or water and were tested in their natural group by a familiar experimenter. All testing procedures were approved by the Leipzig Zoo without a formal protocol number, as the study was not invasive and individuals only participated on a voluntary basis.

Procedure

We used a transparent plexiglass box with one or two platforms in the middle, moving in opposite directions when pulled (Fig. 1; also see Suppl. Mat.). To interact with the box (and to determine which condition was being implemented), subjects had to jump onto one of the two wooden shelves attached to the table legs, one opposite to the other, and visually inspect the set-up, as the platforms and their content were only visible from the shelves. Trials started after the platforms had been baited, when an individual jumped on the subject (*S*)'s shelf. Trials ended when the same individual left the shelf. Only the *S* could pull the platform(s), by pulling the rope (or the platform) with their

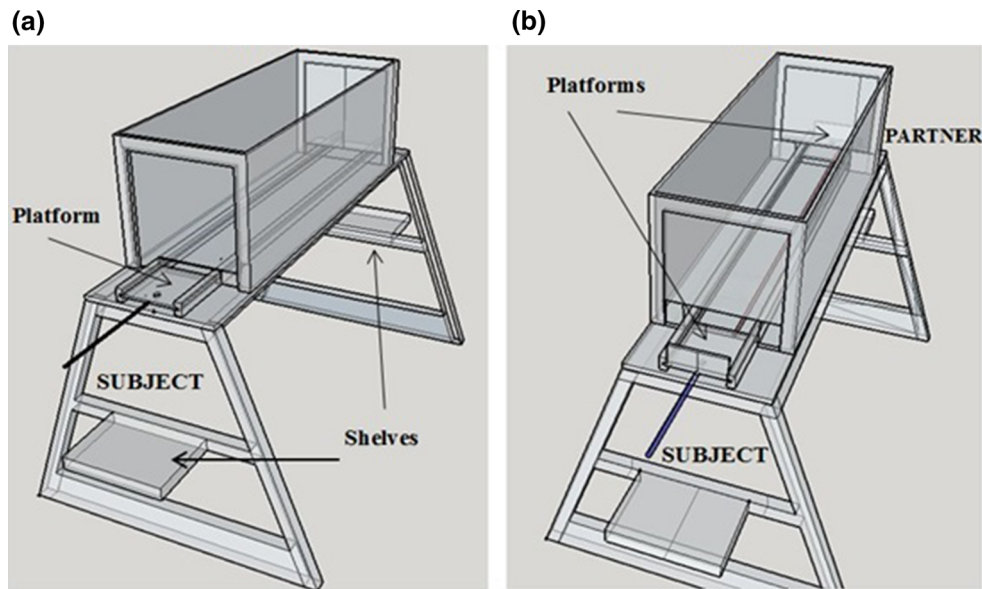


Fig. 1 Pictorial representation of the apparatus used **(a)** in the Habituation conditions (shelves were present for both the subject and the partner to stand, but only the subject's platform was present, and only subjects could thus pull and retrieve food) and **(b)** in the two Partner conditions (shelves were present for both the subject and the partner to stand, and both subject's and partner's platforms were

present, so that depending on the food distribution both subject and partner could retrieve food). In the two No Partner conditions, the apparatus was identical to the one depicted in **(b)**, but the partner's shelf was removed (so that food on the partner's side could never be retrieved)

paws, moving food within reach. In some conditions, a shelf on the partner's (*P*) side could allow a *P* to jump on it and retrieve food from the second platform (Partner conditions); if no shelf was present, no *P* could access the apparatus and retrieve food (No Partner conditions). We refrained from using the more traditional set-up with four baiting locations (in which the *S* would have the simultaneous choice between two pairs of platforms—(1/1) vs. (1/0), wherein the number before the slash represents the food on *S*'s platform and the number after the slash the food on *P*'s platform), as simultaneously assessing the position of food on four platforms might have been cognitively too demanding (see e.g. Cronin et al. 2009).

In the Habituation phase, the *S* and *P* could access the box by jumping on the *S*'s and *P*'s shelves, but only the *S*'s platform was present (Fig. 1a). The Habituation phase allowed individuals in the group to become familiar with the apparatus and its mechanism. At the beginning of each trial, the platform was placed in the middle of the box and baited with a worm. The platform was connected to a rope partially lying outside the box, so that individuals could retrieve the food by accessing the shelf on *S*'s side, pulling the rope (or the platform) with their paws and thus moving the food within reach. The assignment of *S* and *P* was defined by the individual that jumped on the *S*'s shelf and thus became the *S*. During 5 days, seven individuals approached the box and successfully retrieved food by pulling it within reach at least three times. Two further

individuals started interacting with the box at the end of the Habituation phase and also participated in the next conditions. Only these nine individuals (out of the 12-individual group) participated as subjects in the following conditions.

In the two No Partner conditions, we used two platforms but only the *S*'s shelf was available: when the *S* pulled their platform, the platform moved within the *S*'s reach while the other one moved in the opposite direction (where no one could access it). In the No Partner-Self condition, we only baited the *S*'s platform (1/0), so that the *S* maximized food availability by always pulling their platform. In the No Partner-Other condition, we only baited the *P*'s platform (0/1), so that pulling provided food neither to the *S* nor to the *P*: the *P* could not access the apparatus because there was no *P*'s shelf. If individuals understood the mechanism, they should pull less in the No Partner-Other than in the No Partner-Self condition. For 4 days, we administered each No Partner condition for 30 min, randomizing the order of presentation of both conditions.

In the two Partner conditions, we used both shelves and platforms (Fig. 1b). In the Partner-Both condition, both platforms were baited (1/1) and the *S* maximized food income by pulling the platform, thus also delivering food to the *P*. In the Partner-Other condition, only the *P*'s platform was baited (0/1), so that the *S* only prosocially provided food to the *P* if the *S* pulled. If individuals were prosocial, pulling rate should be higher in the Partner-Other (0/1) than in the No Partner-Other (0/1) condition (as only the former

provided food to the *P*). Moreover, pulling rate should not decrease in the Partner-Both (1/1) as compared to the No Partner-Self (1/0) condition (as the additional *P*'s presence should elicit at least the same pulling rate) and the Partner-Other (0/1) condition (if prosocial rather than selfish motivation is the main trigger of pulling). Strategically, the Partner-Other condition allowed the *S* to retrieve the *P*'s food by pulling when no *P* was within 50 cm from the *P*'s shelf and then moving to the *P*'s side to retrieve food (i.e. “selfish trials”). Given that in a group setting no special condition could be run to assess subjects' understanding of the set-up, we considered those “selfish trials” as a measure of *S*'s understanding of the set-up. Special conditions assessing subjects' understanding of the set-up, in contrast, are more easily implemented out of group settings, by isolating individuals and presenting them with the same set-up as in the Partner conditions, but with no conspecific present: if they understand the set-up, they pull the platform delivering food to the *P*'s side, and then go on there to retrieve food themselves (e.g. Stevens 2010; Amici et al. 2014). For 5 days, we administered one daily session consisting of approximately 10 min for the No Partner-Self and 10 min for the No Partner-Other conditions (randomizing the order of presentation across days), followed by 10 min for the Partner-Both and 10 min for the Partner-Other conditions (randomizing the order of presentation across days). In the last 5 days, during 10-minute sessions we administered conditions in a pseudo-randomized order to balance out differences in the number of trials per condition.

Statistical analyses

We video-taped all phases and trials (i.e. 365 trials: Habituation phase = 15% of trials; No Partner-Self condition = 18%; No Partner-Other condition = 24%; Partner-Both condition = 19%; Partner-Other condition = 24%). We coded live the identity of *S* and *P* with a transponder–reader (i.e. by approaching the transponder–reader to the back of the individuals jumping on the shelves, where the transponders were located, and noting down their ID number), whether *S* pulled to move the platform(s) within reach and which individuals retrieved food in each trial (see Suppl. Mat. for the complete dataset). For each condition, we calculated Pielou's *J* as a measure of how equally the trials were distributed across subjects. Pielou's *J* is widely used in ecology to quantify the evenness of species abundance in a certain environment and ranges from 0 (i.e. all trials were administered to only one subject) to 1 (i.e. all subjects in our sample took part in the same amount of trials (see Horn et al. 2016)). As a generalized linear mixed model with binary response (pull/no pull) did not converge, we computed the

mean percentage of pulls across trials for each individual and ran nonparametric two-tailed statistics in R 3.2.3 (R Core Team 2016) to analyse whether our dependent variable varied across conditions (Friedman test, and in case of significance Wilcoxon exact tests for pairwise comparisons). Inter-observer reliability was based on 18% of all trials (Cohen's $\kappa = 0.853$, $n = 67$, $p < .001$). To control for multiple testing, we used the false discovery rate procedure FDR (Benjamini and Hochberg 1995). In the Partner conditions, there were few trials (19.6%) in which no *P* approached, and we thus repeated the analyses including only trials with *P* present. Alpha level was set at 0.05. Below, we marked significant *p* values (based on FDR) with an asterisk and reported *N* values after removing ties. Effect sizes were calculated as Cohen's d_{av} (Lakens 2013).

Results

Understanding of the set-up

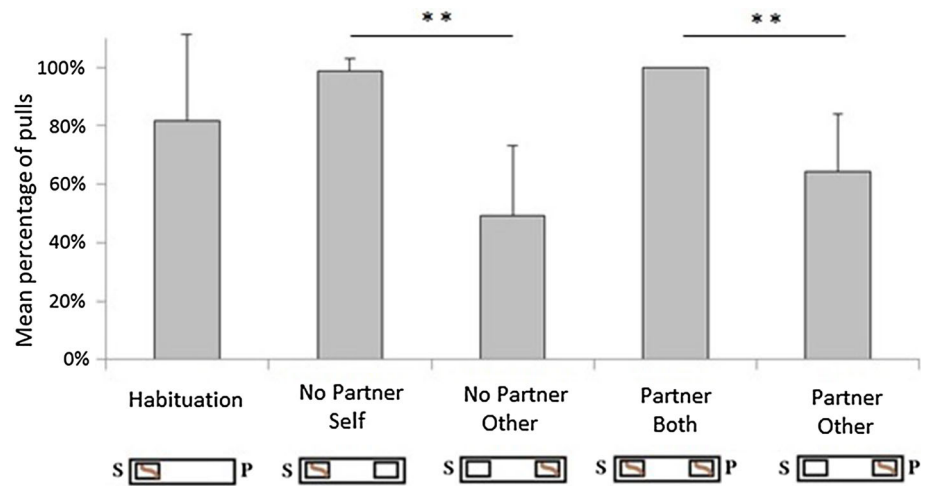
As shown in Fig. 2, meerkats pulled the platform significantly more when they could get the food (1/0, No Partner-Self), as compared to when they could not (0/1, No Partner-Other) ($n = 9$, $T = 45$, $p = 0.004^*$).

Prosociality

Meerkats differed across conditions in the percentage of trials in which they pulled ($\chi^2 = 23.235$, $df = 4$, $p < .001^*$; only if *P* present: $\chi^2 = 22.628$, $df = 4$, $p < .001^*$; see Table 1). They pulled more when doing so provided benefits both to *S* and *P* (1/1, Partner-Both), as compared to when this only provided benefits to *P* (0/1, Partner-Other) ($n = 7$, $T = 28$, $p = 0.016^*$, Cohen's $d_{av} = 1.80$; only if *P* present: $n = 7$, $T = 28$, $p = 0.016^*$, Cohen's $d_{av} = 1.82$). The percentage of pulls was similar regardless of *P*'s benefits, if *S* obtained food (1/1, Partner-Both, vs. 1/0, No Partner-Self; $n = 1$, $T = 1$, $p = 1$), and regardless of *P*'s possibility to access food, if *S* obtained no food (0/1, Partner-Other, vs. 0/1, No Partner-Other; $n = 7$, $T = 22$, $p = 0.219$, Cohen's $d_{av} = 0.47$; only if *P* present: $n = 4$, $T = 20$, $p = 0.844$, Cohen's $d_{av} = 0.22$). An overview of means and standard deviations of pulling rates for all conditions is given in Supplementary Material (Table S2).

“Selfish trials”

There were overall eight instances (i.e. 9% of the trials) in which *S* in the Partner-Other condition (0/1) pulled the platform when no *P* was present, moved to *P*'s shelf and

Fig. 2 Mean percentage of pulls (+SE) as a function of condition**Table 1** Number of administered trials per subject in each condition

Subjects	HB	NPS	NPO	PB	PO
751	9	5	8	11 (4)	16 (2)
758	5	8	11	8 (2)	7 (2)
773	1	1	1	1 (1)	0
774	12	12	33	15 (6)	21 (3)
043	2	3	4	3 (3)	3 (3)
793	6	15	17	16 (4)	16 (3)
798	9	9	4	6 (2)	4 (2)
803	4	8	7	7 (3)	20 (3)
445	6	2	5	2 (2)	2 (3)
Pielou's J'	0.90	0.86	0.85	0.85	0.85

The number of different partners per subject is indicated in parentheses. The last row indicates the evenness of trial distribution denoted by Pielou's J'

HB Habituation, *NPS* No Partner-Self, *NPO* No Partner-Other, *PB* Partner-Both, *PO* Partner-Other

then retrieved food from *P*'s platform. This was done repeatedly by two young high-ranking females (i.e. in 43 and 14% of the trials they took part in), and once by two older males. However, the same individuals also pulled in trials with *P* being present and never postponed their pulls until there was no *P* on the opposite shelf. Although we had no statistical power to detect possible differences between the individuals clearly understanding the set-up (i.e. pulling the platform in “selfish trials”) and the other individuals, both groups appeared to pull with a similar frequency. Notably, individuals clearly understanding the set-up pulled less than the others in the Partner-Other (0/1) condition. Moreover, they pulled with very similar rates in the Partner-Other (0/1) and No Partner-Other conditions (0/1), as well as in the Partner-Both (1/1) and No Partner-Self (1/0) conditions (see Table S2 in Suppl. Mat.).

Evenness of trial distribution

As given in Table 1, the trials in all five conditions were evenly distributed across subjects, with Pielou's J' ranging between 0.85 and 0.90. The distribution of individuals being the partner in the Partner-Both and Partner-Other conditions was less even, with Pielou's J' being 0.60 and 0.41, respectively (see also Table S4 in Suppl. Mat.).

Discussion

In the Habituation phase, meerkats pulled significantly more in the No Partner-Self (1/0) than in the No Partner-Other (0/1) condition, although the total amount of food on the platforms was the same. However, meerkats did not prosocially donate food to partners. Although subjects always pulled in the Partner-Both condition (1/1), the percentage of pulls significantly decreased in the Partner-Other condition (0/1). The opportunity to provide food to partners (i.e. whether there was a shelf and food on the other side) had no effect on the percentage of pulls, as subjects pulled with the same frequency in the No Partner-Self (1/0) and Partner-Both (1/1) conditions, and in the No Partner-Other (0/1) and Partner-Other (0/1) conditions. This suggests that the decision to pull was based only on the presence of food on the subject's side, and not on the benefits they could provide to partners. Moreover, in “selfish trials” some subjects moved to the partner's side to purposefully retrieve food from there, confirming that at least a subset of subjects understood the set-up, but were only trying to maximize their own benefits.

Why do cooperative breeding meerkats actively donate food to pups in the group (Brotherton 2001), but failed to be prosocial in our experimental set-up? One reason may be that subjects simply failed to understand our set-up. Indeed, meerkats pulled based only on the presence of food

on their side, either because they were indifferent to the partners' benefits, or because they did not understand that pulling from their side also provided benefits to the partner. To exclude this last explanation and confirm that meerkats understood the set-up, it would have been necessary to individually test subjects by positioning food only on the partner's side, in the absence of partners, so that subjects had to pull the platform from their side to retrieve food from the opposite side. However, this is exactly what happened in the Partner-Other condition, when no partner was on the shelf—in some trials, meerkats pulled from their empty side and retrieved food from the opposite one, suggesting that at least some subjects really understood the set-up. Importantly, the behaviour of these individuals pulling in the “selfish trials” did also not show evidence of prosociality, as their behaviour in the Partner-Other (0/1) and No Partner-Other (0/1) conditions did not differ.

A second possible reason why meerkats failed to be prosocial in our task may be that meerkats are prosocial in natural contexts, but not in experimental set-ups. Jackdaws (*Corvus monedula*), for instance, are known to actively share food in the wild (de Kort et al. 2006; von Bayern et al. 2007), but not in an experimental set-up similar to the one used in this study (Schwab et al. 2012). In particular, our set-up used visible food rewards which may elicit selfish and competitive behaviour (Hirata 2007; Horner et al. 2011). In addition, it may be cognitively demanding since it requires individuals to move away food when donating. However, this task has successfully elicited prosocial behaviour in other species (e.g. common marmosets: Burkart et al. 2007; Lakshminarayanan and Santos 2008; Takimoto et al. 2010), and in natural settings, animals must move visible food away from themselves when they give it to others.

A third possible reason may be that meerkats prosocially give food only to young pups (see e.g. Izawa 1978; Rapaport and Ruiz-Miranda 2006). In cooperative breeders, active transfers of food are largely limited towards young infants and strongly decrease when pups get older (e.g. meerkats: Brotherton 2001; cotton-top tamarins: Joyce and Snowdon 2007), suggesting that active food transfers may only happen to specific partners and during a limited developmental period. In meerkats, in particular, adults rarely share food with each other (e.g. Clutton-Brock and Manser 2006), and even pup begging calls only induce food sharing towards pups, but not towards other group members (Madden et al. 2009). Alternatively, the presence of new pups may alter the hormonal profile in all group members, triggering a “prosocial effect” which affects behaviour towards all group members. Therefore, meerkats would prosocially give food to all group members, but only when young pups are in the group (but see e.g. Burkart and van Schaik 2013, for evidence of prosociality in primates

with no young offspring in the group). In common marmosets, for instance, oxytocin levels (which are positively involved in the regulation of mammal parenting and social bonding) increase in all group members when infants are born (Finkenwirth et al. 2016). Also in meerkats, prosocial behaviour towards pups is strongly regulated by hormones (e.g. Carlson et al. 2006a, b; Soares et al. 2010; Madden and Clutton-Brock 2011; Santema et al. 2013). Therefore, it is possible that meerkats tested with this set-up would have behaved more prosocially if young pups were in the group.

Thus, the behaviour of meerkats did not conform to the predictions derived from the cooperative breeding hypothesis. It may be that the cooperative breeding hypothesis is only supported when the efforts needed are too high to be made by only one individual (e.g. digging burrows, guarding) or when the value of the resource is pitted against the recipients' vulnerability (e.g. protecting or donating food to pups until they are autonomous). After all, being cooperative breeders implies the presence of adults and pups, and hypotheses predicting their behaviour may only work if both are present. Further studies should investigate whether hormonal levels and the presence of vulnerable subjects in the group during the testing period are needed to trigger prosociality.

Finally, it is interesting that in “selfish trials” individuals pulled the platform when no partner was present and then retrieved the partner's food. However, meerkats also pulled in trials in which partners were present and then unsuccessfully tried to reach for the food by running to the partner's shelf, failing to wait and pull when partners left. Moreover, individuals in this condition pulled as much as in the No Partner-Other condition (i.e. when retrieving the food was impossible), showing that individuals did not learn to use this strategy to maximize their food income.

To conclude, in order to understand why meerkats failed to be prosocial in our task, more studies are needed, including (1) a larger number of individuals (given that effect sizes are usually small even when statistical significance is obtained: Cronin 2012), (2) finer-grained analyses at the dyadic level (given that prosociality may appear in few specific dyads) and (3) different methodological approaches, including set-ups in which individuals are close to each other, and not in front of each other (see Cronin et al. 2010; Amici et al. 2014). However, it is noteworthy that a species showing such a wide range of prosocial behaviours in the wild does not significantly extend prosocial behaviour in a new experimental context, at least when no pups are in the group.

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Compliance with ethical standards

Conflict of interest All authors declare they have no conflict of interest.

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