

# 13 Meerkats – Identifying Cognitive Mechanisms Underlying Meerkat Coordination and Communication: Experimental Designs in Their Natural Habitat

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## Species Description

### Anatomy

Meerkats are small carnivores with an average adult mass of 700–800 g in their natural habitat. They are about 35 cm in height when standing up on their hind legs, which they do often in a range of behaviours, including sunning, bipedal vigilance and sentinel duty. Their tail enables them to stand bipedal for extended periods on the ground and also to balance when climbing up into shrubs or trees to act as sentinels. Digging is one of the main activities of meerkats to find prey in the sand (Doolan and MacDonald, 1996), to renovate their sleeping burrow entrances (Bousquet, 2011) or to clean out boltholes, which they use as shelter from predators (Manser and Bell, 2004). This has resulted in the evolution of strong forearms with elongated nails (up to 2 cm), enabling them to efficiently push away large amounts of sand.

Meerkats are well-camouflaged with the colour of their fur adjusted to the habitat they live in. They range from dark brown in the green scrubland (e.g. in Addo National Park) to light brown in the Kalahari (pers. obs.). The pattern of dark stripes on their back is unique and can be used for individual recognition. The belly is typically darker than other parts of the body and can be used to efficiently absorb heat from the sun. In the coldest times of the year, they stand with their belly directed towards the sun for up to an hour at the sleeping burrow entrances before they start foraging for the day. During the cold season, their hair grows much longer and denser. However, temperature regulation has its limitations during the hot periods of the year: meerkats stop foraging in the open when sand surface temperatures rise above 60°C and also stop foraging in the shade when air temperatures in shaded areas rise above 40°C.

### Perception

Meerkats have evolved an elaborate vocal and olfactory communication system, and also use visual signals quite extensively. The range of frequencies in the different call

types seems to be within the human hearing range (i.e. 20–20,000 Hz). Most of the tonal calls have a fundamental frequency of 200–300 Hz and a bandwidth of up to 4–8 kHz, while the noisiest broadband calls can range from low frequencies up to 20 kHz and potentially even above (Manser, 1998; Manser *et al.*, 2014). Currently, little is known about the hearing abilities of meerkats, including peak auditory sensitivity. Most calls likely have a transmission range between 10 and 30 m, although the noisiest broadband calls may carry further, with barks (Townsend *et al.*, 2014) potentially carrying up to 100 m, depending on environmental conditions.

Meerkats, like many mammals, rely heavily on smell, and in comparison to most other social mongoose species, their nose appears substantially elongated. This may be an adaptation to smelling in the digging holes for tunnels made by prey items, but may also allow them to perceive subtle vibrations when digging. Meerkats mark their territory with faeces, urine, scent marks and, to a lesser degree, saliva. Scent glands are located on their cheeks, along the side of their body and in the anal region. Olfactory signals and cues play a crucial role in meerkats, to which they may respond from several metres away, often recruiting others to the location by vocal and visual signals (e.g. recruitment calls or aroused body posture with tail up and hair erected; Manser *et al.*, 2001). Moreover, olfactory cues allow them to distinguish group members from non-group members (Mares *et al.*, 2011) and kin from non-kin (Leclaire *et al.*, 2013).

In regards to visual signals, little is known about colour or depth perception in detail (Moran *et al.*, 1983). However, based on our field observations, their eyesight is extremely adapted to detect and identify objects at far distances in the sky, and also in open and structured habitats. For example, meerkats will produce alarm signals in response to dangerous predators, such as a martial eagle, at distances over 1 km away (when they might not even be visible to humans with binoculars). However, they will not respond to a white-backed vulture of similar size and colours at the same distance (Kalahari Meerkat Project (KMP), unpublished long-term data). Meerkats can also look directly into the sun and still reliably detect objects in the sky. They appear to have poor visual perception of close objects and often fail to detect non-moving prey items at close distances if they do not stand out obviously against their background. However, meerkats seem to be very good at perceiving contrasts and can immediately detect anything moving, whether it is close by or at a far distance.

## Life Cycle

Meerkats live in groups of 3–50 individuals, where mainly the dominant pair reproduces and the other group members help in raising their offspring (Clutton-Brock *et al.*, 2010). After birth, pups spend 3 weeks underground in their burrow, typically being looked after by one or two babysitters, while the rest of the group is foraging (Clutton-Brock *et al.*, 2001a). After having emerged, pups spend another week at the birth burrow and only then start to join in foraging with their group, being fed prey items by older group members (Brotherton *et al.*, 2001). They also start digging for prey themselves, and at the age of 3 months they find food rather independently, and pup feeding ceases completely (Thornton, 2008). When they are 6 months old, they have

developed the behavioural repertoire of an adult meerkat, such as producing alarm calls (Hollén *et al.*, 2008), performing sentinel behaviour or also sometimes staying behind at the birth burrow as a babysitter. They usually become sexually mature around 1 year of age.

Males disperse voluntarily from their natal group when they are about 1.5–2 years old (Young *et al.*, 2007), while females do not leave unless they are forced out by the dominant female (Stephens *et al.*, 2004). These periods of conflicts provide very good opportunities to test their social knowledge and understanding of their social environment. Subordinate males, when starting to disperse, typically ‘rove’ for some weeks or months, temporarily leaving their natal group to explore other groups for mating opportunities or to immigrate. During this period, they seem to invest more into their own growth than performing cooperative tasks, as they are not able to maintain their energy expenditure with their limited foraging opportunities when by themselves on their roving excursions (Young *et al.*, 2007). Subordinate females are frequently attacked by the dominant female, especially in the second half of her pregnancy. During these periods, subordinate females try to either avoid the dominant female or show pronounced submission behaviour, including submission calls (Kutsukake and Clutton-Brock, 2006; Reber *et al.*, 2013). These behaviours seem to reduce the level of conflict and potentially delay the eviction by the dominant female.

### Individual Identification

Each individual meerkat develops its own specific fur colouring with distinctly patterned dark stripes on their back, and the sexes are easy to distinguish due to the large testes in males. However, if wild individuals need to be distinguished in groups of more than five individuals from several metres away, excellent observation skills and memory are required. An effective solution is therefore to mark them with unique patterns of hair dye marks (which need to be reapplied every 2–3 weeks) at specific locations of their body (Jordan *et al.*, 2007; Figure 13.1). This ensures more reliable data collection, especially when several groups are studied by many different researchers. We also implant every meerkat with a transponder chip to ensure life-long identification (Jordan *et al.*, 2007); for example, if a meerkat is not seen for a long period of time due to dispersal or roving, and the hair dye mark disappears. Ear tags are not very effective, as meerkat ears are very small and tags get quickly lost. Similarly, we also tried freeze-branding, as done in other small mammals, such as ground squirrels (Waterman, 2002), but this is a rather invasive and unreliable method, which we do not use anymore. A skin sample is also collected from every meerkat captured from the population in order to determine the genetic relatedness of the different individuals (Griffin *et al.*, 2001).

### Ecological Characteristics

Meerkats live in the dry semi-desert of the Kalahari in the southern part of Africa, including Botswana, Namibia, South Africa and the very southern tip of Angola. In the Kalahari, the climate includes the warm and wet season from October to April



**Figure 13.1.** Meerkats in the southern Kalahari, being habituated to close observation, coordinate their group activities with vocal, olfactory and visual signal, and rely greatly on social learning. The second meerkat from the left carries a radio collar with a VHF transmitter, which allows finding the group at any stage. For individual recognition, meerkats are marked with hair dye at specific body parts (e.g. the one on the front to the right has a dark spot on the right shoulder). Photo taken by M. Manser.

(with little rain from October to December, and more rain from January to April) and the cold and dry season from May to September. During the warm season, and in particular from November to February, the meerkats get up with sunrise and start foraging more or less immediately until it gets too hot, then they rest under vegetation or in boltholes from around 10 AM to 6 PM, after which they forage for another hour until sunset, and finally disappear into their sleeping burrow. During the cold season, 20–60 minutes of sunning behaviour precedes foraging, which usually continues until sunset with a few short breaks in between.

At the study site of the KMP, the habitat consists of large, open, sandy areas, in particular along dry riverbeds, interspersed with large areas of bush (e.g. *Rhigozum* shrub). Meerkats prefer to forage in more open vegetation (i.e. below 1.5 m), where visual contact and call transmission are facilitated. Meerkats have many different aerial and terrestrial predators (Clutton-Brock *et al.*, 1999a), which have caused them to evolve a highly efficient anti-predator sentinel system (Clutton-Brock *et al.*, 1999b), which allows them to warn each other with alarm calls specific to the type and urgency of the threat (Manser, 2001).

The main food sources (including insect larvae, scorpions, spiders, barking geckos) need to be dug out of the sand, while some beetles and small reptiles are caught on the surface (Doolan and MacDonald, 1996). Large millipedes, tortoise eggs or pygmy mice can also be dug up, mainly from bolthole entrances, and lizards and small snakes can be caught and eaten. The majority of their active foraging time is spent palpating the soil surface, likely for entrances of animal tunnels or other disturbances of soil structure hinting towards prey location. Once they have located a promising spot, they then start to dig at this specific location and sometimes need up to 20 minutes to get the prey, creating holes down to

80 cm into the sand. Adults do not share food among each other, and pregnant or lactating dominant females often compete with subordinates for access to promising foraging holes (Flower, 2011b). However, food is shared with pups, until they have learned to forage independently by the age of 3 to 4 months (Brotherton *et al.*, 2001).

## Social Characteristics

Meerkats are characterized by a clear dominance structure, with the dominant pair being the main breeders and other group members helping to raise their pups (Clutton-Brock *et al.*, 2001b). Within the subordinates, hierarchy is based on age, and in females on body size (Thavarajah *et al.*, 2014). Group members are typically highly related to each other, with the dominant pair, their offspring, and potentially one or a few unrelated immigrated males (Clutton-Brock *et al.*, 1998). Females are not accepted as immigrants into existing groups.

Except for roving males or subordinate females evicted by the dominant female, meerkats are always found in groups (Young and Monfort, 2009). Separation from the group is one of the most stressful situations for meerkats, and they have evolved an efficient vocal system to keep cohesion while foraging or to find each other when temporarily lost (Manser, 1998; Manser *et al.*, 2014; Gall and Manser, 2017).

During dominance competition, dominant individuals may evict same-sex subordinates that might threaten their position. In the wild, this occurs more frequently among females, with aggression increasing when the dominant female is pregnant (Young *et al.*, 2006). In males, it only occurs under specific group compositions, when the dominant male has a brother of similar age and weight, and both of them are immigrants and unrelated to the females in the group (KMP, long-term data).

## State of the Art

Studies on meerkat cognition have addressed several aspects of physical and social cognition, with a special focus on group coordination (Bousquet *et al.*, 2011; Gall and Manser, 2017), vocal (Manser *et al.*, 2014) and olfactory (Leclaire *et al.*, 2013) communication, social learning and teaching (Thornton and Clutton-Brock, 2011). On the immediate level, group coordination in meerkats is largely achieved through vocal and visual communication. Vocal signals have been better investigated, because they are easier to identify and simulate, but also because meerkats have a large vocal repertoire, with more than 30 different discrete call types used for group cohesion, anti-predator behaviour, division of cooperative tasks and social interactions (Manser, 1998; Manser *et al.*, 2014).

## Group Coordination and Communication

Meerkats forage as a cohesive unit throughout the day, and they emit several different call types to maintain group cohesion during their foraging excursions. ‘Lead’ and

‘move’ calls are given to coordinate departure from the sleeping burrow and to induce group members to switch foraging patches (Turbé, 2006). If more than three individuals are involved in emitting ‘move’ calls, the group moves to the next foraging area, but if just one or no individual replies to the call, the group usually continues to forage on the current foraging patch, suggesting that a quorum has not been reached (Bousquet *et al.*, 2011). While meerkats are foraging, they regularly emit soft ‘close’ calls, which are likely to maintain contact among the dispersed group members, and space themselves out to avoid frequent food competition (Manser, 1998; Engesser, 2011). Individuals that get separated from the group emit soft ‘alert’ calls, which turn into loud barks if they cannot see the group. Barking causes other group members to stand bipedally or to move in the direction of the lost animal (Manser, 1998).

Individual meerkats frequently stop foraging and move to a raised position where they scan the sky and surrounding area for predators (Clutton-Brock *et al.*, 1999b). Although there is no predictable rotation in sentinel behaviour, individuals alternate and typically avoid going on guard when another individual is already acting as a sentinel (Clutton-Brock *et al.*, 1999b; Manser, 1999). Individual contributions to sentinel duty vary and are positively associated with age, weight and foraging success, and are higher in males than females or after being artificially provisioned (Clutton-Brock *et al.*, 1999b). Average contributions to sentinel duty increase when the risk of predation is high, and also when pups are foraging with the group (Santema and Clutton-Brock, 2013).

When meerkats detect danger, they give alarm calls, which vary in their acoustic structure both in relation to the type of predator they have seen and to the urgency of the danger (Manser, 2001; Manser *et al.*, 2001, 2002). The likelihood of alarm-calling depends on whether other group members are close by (Townsend *et al.*, 2012). So far, we have no evidence that receivers adjust their response to the identity or reliability of the caller, possibly because the costs of ignoring alarm calls are too high (Schibler and Manser, 2007). However, receivers habituate to playbacks of alarm calls quite fast, and after the second or third playback they do not respond as intensively anymore if no actual predator approaches within a short period after having heard an alarm call (Karp *et al.*, 2014). Sentinels give regular high-pitched calls when they are on ‘watch’, which are perceived by other group members, allowing them to reduce their level of vigilance while foraging (Manser, 1999; Rauber and Manser, 2017).

Vocalizations also play an important role in regulating social relationships within groups. Meerkats express their affiliative or aggressive intentions when approaching each other with appropriate calls. Growls reflect aggression and are given by dominants to subordinate individuals, or during food competition by all individuals involved. Subordinates express their submission with higher-pitched, more tonal submission ‘grovelling’ calls (Kutsukake and Clutton-Brock, 2006). Furthermore, close calls are used to regulate (Gall and Manser, 2017) and monitor other individuals’ movements (Townsend *et al.*, 2011). Responses to calls are adjusted to social circumstances. For example, subordinate females that experience aggression from the dominant female and are at risk of being evicted respond very strongly to aggressors’ calls (Reber *et al.*, 2013).

Olfactory communication plays a role in inter- and intragroup communication, and several different types of media, including faeces, urine, gland secretions and even saliva are used to advertise the use of a territory (Jordan *et al.*, 2007). These signals include individual signatures, and allow the receivers to not only gain information on the identity of the territory owner, but also on kinship (Leclaire *et al.*, 2013). They are likely also used for intragroup communication. As for vocal communication, experiments suggest that receivers discriminate at the individual level and may maintain representations of the signal producer (Reber *et al.*, 2013).

### Social Learning, Traditions and Teaching

As expected for cohesive living species with sharing cooperative tasks, meerkats rely on social learning. This is particularly obvious in the context of learning about foraging and likely also occurs in the context of predator recognition and spatial mapping of their home range. For animals relying on food which can vary depending on season or vegetation type and could even be poisonous, it is of advantage to learn early which food items are appropriate. In meerkats, young individuals follow the older group members and get fed in their first 2–3 months, while joining the foraging group. Thereby, they learn about edible food. Meerkats seem particularly neophobic to new food types and only eat what they have seen conspecifics eating (Thornton, 2008). However, we know less about how much they learn about predator recognition, shelter location or their territory in general. Current observations show that, when recognizing danger, pups up to 4–5 months largely rely on following older group members' responses (Hollén and Manser, 2006; Graw and Manser, 2007). Similarly, offspring seem to run independently to the shelter without prompting only after about 4–6 months of age (Manser and Bell, 2004), although we do not know how they learn about it.

In meerkats, there is evidence of tradition establishment. When specific individuals in a group are trained as demonstrators to be rewarded at landmarks characterized by a specific symbol, naïve individuals are more likely to approach landmarks of that type and obtain the rewards following encounters with demonstrators (Thornton and Malapert, 2009). However, individuals that learn that one type of landmark is profitable also begin to investigate the landmarks characterized with other symbols, and traditions to approach a specific symbol collapse over time. Other evidence for conservative traditions in meerkats is based on the observation that differences persist between neighbouring meerkat groups, in terms of emergence time from their sleeping burrow in the morning (Thornton *et al.*, 2010). Over an observation period of 11 years, some groups consistently emerged later in the morning than others, even when group membership changed (e.g. change in dominance or after immigration of males).

Moreover, meerkats show the different steps that are involved in animal teaching (Thornton and McAuliffe, 2006; Thornton and Raihani, 2010), according to the definition by Caro and Hauser (1992). When it comes to pup provisioning, group members adjust their behaviour to the age and experience of pups to enhance the pup's foraging skills. They feed the very young pups with dead or badly wounded prey and then



gradually provide them with fully alive prey, which is able to escape or strike back (Thornton and McAuliffe, 2006). For example, scorpions are initially presented to pups when dead or wounded, with their stings removed, but as pups grow up, they are gradually presented with intact scorpions, which pups learn to kill after removing their sting. Experiments confirm that presenting pups with active prey improves the rate at which they learn handling skills at some cost to helpers, and consequently represents an example of teaching behaviour. In addition, helpers preferentially feed rarer food items to pups, which may help to broaden the range of food types they will eventually use (Thornton, 2008).

### All for One and One for All

#### Box 13.1 Cooperative Breeding and Cognition

*Judith M. Burkart*

Like meerkats, callitrichid monkeys are cooperative breeders. They live in extended family groups, often complemented by immigrants, and all group members help raising the offspring (Erb and Porter, 2017). Also like meerkats, they have an elaborate vocal communication system (Snowdon, 2017) and are amenable to studies investigating cognitive mechanisms underlying vocal communication. Such efforts can build on rather solid knowledge of their perceptual capacities, including their hearing range (Osmanski and Wang, 2011) or colour vision system (Kawamura, 2016), and an increasing number of studies documenting their social and non-social cognitive skills (Schiel and Souto, 2017).

The breeding pair typically monopolizes reproduction (Yamamoto *et al.*, 2014), but behaviourally, this does not translate in marked dominance hierarchies. In fact, it is often not possible to establish clear dominance hierarchies within groups, because aggression is rare and interactions are highly tolerant (Schaffner and Caine, 2000). Accordingly, among primates, allomaternal care and thus cooperative breeding is associated with high social tolerance and proactive prosociality (i.e. a motivational concern for not only one's own but also others' welfare), as shown by comparative analyses over a large number of species (Burkart *et al.*, 2014). As a result of these predispositions, callitrichids tend to excel in socio-cognitive tasks, but perform just regularly in non-social cognitive tasks (Burkart and van Schaik, 2010, 2016). These results are highly relevant for biological anthropologists interested in human cognitive evolution (Hrdy, 2009; Burkart *et al.*, 2009; Tomasello and Gonzalez-Cabrera, 2017), because humans are the only other cooperative breeders among primates (even though some level of allomaternal care is widespread in this taxon).

A potential link between communicative complexity and cooperative breeding has been proposed by several researchers (e.g. Snowdon, 2001; Burkart *et al.*, 2009; Zuberbühler, 2011; Borjon and Ghazanfar, 2014; Leighton, 2017) and may be important to understand language evolution. Such a link may arise when proactive



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prosociality is also expressed as information donation, when the coordination of cooperative care activities has to be fine-tuned via communicative signals, and when immatures use communicative signals to engage caregivers (Burkart *et al.*, in press).

Importantly, to systematically test for consequences of cooperative breeding, it is not enough to investigate cooperative breeders only. Rather, species with and without cooperative breeding need to be compared, while controlling for confounding factors such as brain size, ecology and phylogenetic relationship. Ideally, this is achieved with broad phylogenetic comparative analyses (Burkart *et al.*, 2014; MacLean *et al.*, 2014).

When broad phylogenetic comparisons are not possible, targeted contrasts provide a good approximation (MacLean *et al.*, 2012). Here, closely related taxa are compared that are as similar as possible to each other, but differ in their breeding system. In primates, this includes contrasts between the cooperatively breeding callitrichids versus their closely related but independently breeding sister taxa, the cebid monkeys; siamangs (high levels of allomaternal care) versus gibbons (low levels of allomaternal care); and humans (cooperative breeders) versus chimpanzees and bonobos (our closest related sister taxa, without cooperative breeding; Burkart and van Schaik, 2010). Variation in breeding system in mongoose species offers the opportunity to test additional contrasts outside primates.

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## Field Guide

### Habituation to Human Observers

Although observing the natural behaviour of a species can be informative about the potential of underlying cognitive mechanisms, experiments with controlled conditions are needed to disentangle potential alternative processes being involved. One requirement to experimentally test individuals is that subjects are relaxed and not distracted. This requires either remote-controlled experiments, which can also be observed and documented from a distance, or habituation to a level when the presence of an experimenter/observer no longer influences the animals' behaviour. Although remote-controlled experiments ensure that the test set-up is not influencing any aspect of the response, they do not facilitate spontaneously adjusting experimental set-ups to a given situation. This makes it particularly difficult for experiments in the wild, as the surroundings cannot be completely influenced and controlled during the experimental phase. These problems can be largely overcome by habituating meerkats to the presence of humans. In our KMP population, all group members are habituated to humans, walking behind them within a distance of 1 m and moving objects such as microphones even closer (Figure 13.2).



**Figure 13.2.** Observer recording habituated meerkat when guarding, while the rest of the group is foraging.

Photo taken by Jörg Niggli.

The process of habituating a completely wild group of meerkats can take up to 15 months, depending on their previous encounters with humans. Habituating meerkats in the Kgalagadi National Park, where people are not allowed to leave the car, often only took up to 3 months. In contrast, at the KMP (established on farm land about 200 km outside the park), it took up to 15 months. This can be explained by the fact that at the KMP the meerkats were often chased by humans, and wild groups run away as soon as they see us approaching from a distance as far as 300 m. The habituation process starts with sitting at a far distance (about 30–50 m) from their sleeping burrow, before they start to emerge in the morning. The wild meerkats will then watch us constantly from their safe burrow entrances for up to 2 hours, before leaving the burrow system from the most distant burrow entrance, where all of them run off at high speed to start foraging at some distance away. By more or less finding the group again at their sleeping burrows every day (at the beginning with the help of a local tracker, following their tracks to the sleeping burrow in the evening, later on by capturing an adult individual and putting on a VHF radio transmitter; Jordan *et al.*, 2007), we can slowly progress in sitting closer to the group and gently moving our body parts. Only once we can sit with most of them within 5–10 m, we start standing up and moving around slowly. This may happen after 6–8 months of habituation. The next large step is to try to follow the meerkats when

they leave for foraging. For them, this means giving up the safety of the burrow entrances, and it takes quite a long time for them to trust us in this situation.

In general, meerkats are easily scared by abrupt movements and loud sounds. We repeatedly emit soft calming sounds when working with them, especially when we change our activity or move in their close surroundings. Also, when we approach a group, we produce these sounds, identifying us as non-dangerous humans. Individuals differ widely in how quickly they accept our presence and following behaviour. In a group of mainly habituated individuals, a less well-habituated meerkat can be approached quite closely by looking in the direction of another meerkat and moving slowly backwards towards the nervous individual: typically nervous meerkats seem to perceive this, as if the human's focus were on the other conspecific. The most important 'skill' in habituation is to observe the behaviour of each individual, and adjust our own movements and behaviour to the habituation level and response of the meerkats. Also, wild animals respond negatively to direct eye contact. However, this reaction appears to cease once meerkats are highly habituated.

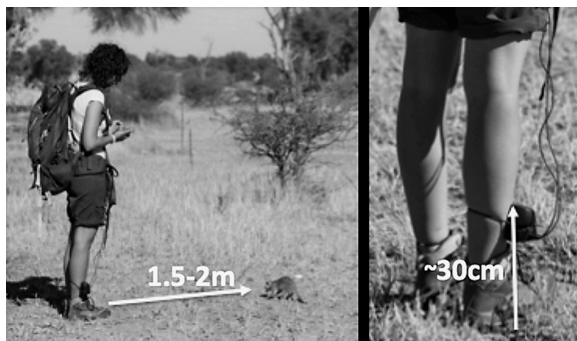
## Experiments

In their natural habitat, habituated groups of meerkats are most relaxed early in the morning or during summer time over lunch breaks. However, when they first emerge from their burrows, they look around nervously and scan their surroundings constantly. After some time, particularly when many other group members are up, they relax and still remain at the burrow, to warm themselves in the sun. During summer, these periods before foraging are typically short, but meerkats stop foraging for extended periods over the hot lunch periods. If they stay above ground, they lay in the shade and socialize, behaving very relaxed. These periods at the morning sleeping burrow or during lunch breaks are the times when it is best to perform problem-solving experiments, which take slightly more time (Thornton and Samson, 2012) than playback experiments or simple presentations of olfactory cues. Meerkats will be attentive and motivated, and not distracted by other group members' activities.

During foraging, in contrast, meerkats are constantly moving and strongly focused on finding prey items and maintaining group cohesion. Therefore, it is difficult to test meerkats individually for more than a minute, as target subjects become anxious and try to rejoin the group. However, it may be possible to test them by trying to predict their movement direction, as individuals may separate from the group for up to 5–10 m during foraging. A more active way to separate animals up to 30 m from the group is to lead them away with a scorpion, hanging it down on a fishing line in front of the meerkat's head (Zöttl, 2009). You can then present the test stimuli, although this brings up a general problem within experiments in relation to food rewards. Guiding meerkats to a certain location with food may strongly focus their attention on the food, rather than the intended test stimuli. Even during testing, if repeated food rewards are part of the experiments, subjects may focus more on the food than on the actual experimental stimuli presented.

In many ways, meerkats are ideal subjects for experiments that involve presentations of acoustic, olfactory or visual stimuli. We have performed many manipulations in the context of predator perception and responses, and more recently we have also experimentally tested the underlying cognitive mechanisms in spatial coordination and their social knowledge. As most of the vocalizations are soft and given over short distances, small loudspeakers (e.g. iHome rechargeable mini speaker, iHM79SC; Rauber and Manser, 2017) can be used, hiding them behind vegetation or otherwise easily camouflaging them. More recently, we often fix the loudspeaker to the leg of the experimenter, enabling broadcasting to occur at the height of a foraging or bipedal standing meerkat (Reber *et al.*, 2013; Figure 13.3). This allows fast adjustment to a changing context, which is particularly necessary during the constant movements of foraging meerkats. The presentation of olfactory cues, e.g. faeces or gland secretions, is best done by placing the stimulus next to (within 20–50 cm) a digging meerkat, without interrupting its activity (Leclaire *et al.*, 2013; Zöttl *et al.*, 2012). When the meerkat finishes digging, it will then likely attend to the sample, if it is of any interest to it. Visual stimuli, such as stuffed predators, kites or remote-controlled airplanes (to simulate raptors flying in), can be presented to meerkats at their morning sleeping burrows or also during foraging. Particular care has to be taken to do all the preparations before the group emerges, or to perform them in a calm manner if presentations will occur during foraging, to avoid meerkats associating these manipulations with us. Before testing occurs, any new objects that have to be brought in for the experiments (e.g. a hide for concealing a predator) must be shown to the meerkats in previous sessions, so that they can be habituated to the point where they do not respond to these objects anymore (this typically only takes one or few presentations).

Some caution needs to be taken with regards to habituation to experiments (i.e. not attending to them anymore), and also to how differences in their ecological and social environment can affect the responses to stimuli. We have experienced that the intensity of meerkat responses to presentations of acoustic, olfactory and visual stimuli decreases



**Figure 13.3.** Playback set-up: experimenter following within a few metres of the test subject, with loudspeaker fixed to the leg at the height of a guarding meerkat.

Photo taken by Gabriela Gall.

quite fast if they are repeated more frequently than the natural occurrence rate of these situations in the wild (Schibler and Manser, 2007; Karp *et al.*, 2014; Voellmy *et al.*, 2014). We therefore have restrictions on how often such experiments can be performed in a group or to a specific individual, depending on the stimuli type, and also whether it induces a response from only the target subject or from the whole group. For example, close calls, the frequently emitted contact call produced every 4–20 s during foraging, can be played back more often than an alarm call, which potentially only occurs a few times per foraging session. In general, we limit experiments on the same group to every other day, and while close calls can be tested during each experimental trial, alarm calls can only be tested once per week, although within a session we may playback more than one alarm call or bout of alarm calls, depending on the experimental design and question. The same rules apply when deciding how frequently olfactory (Zöttl *et al.*, 2012) and visual stimuli (Thornton and Malapert, 2009) can be presented to a specific individual or group. These precautions are taken to avoid getting our groups used to experiments to the point where they no longer respond, or provide less-intense responses due to repeated exposure.

Moreover, it needs to be considered that even small differences in the context may trigger variation in their responses. In playback experiments during foraging, for instance, meerkats digging for a specific prey will be less responsive to the same call type than meerkats searching for prey or prey cues, such as tunnels (Amsler, 2008). This is also true when presenting olfactory or visual cues to meerkats. A meerkat digging for prey is focused on the task of obtaining that food item and is much less attentive to its environment. As a consequence, the stimuli should only be brought in to non-digging individuals, or in such a way that, when the target subject finishes digging, it will then be easily exposed to the well-placed stimuli. Also, meerkats close to shelter, such as sleeping burrow entrances or boltholes, will respond to stimuli more slowly or with less intensity than meerkats out in the open and far away from shelter options, particularly if predator-related stimuli are being tested (e.g. sentinels, typically located next to a bolthole, take longer to leave their position than foraging meerkats further away from shelters; Clutton-Brock *et al.*, 1999b). Furthermore, the social context in social species needs to be taken into account during testing: a group in a socially stable phase provides a rather different test environment than a group where social tension occurs (e.g. when the dominant female is pregnant). For example, subordinate females change their behaviour into submission when they hear that the dominant female is close by, but only during periods of ongoing social conflict between them (Reber *et al.*, 2013). These different conflict situations allow several opportunities to test cognition in different contexts.

As cooperative breeders, meerkats are a model species to investigate questions on prosociality and cooperation. By showing a high reproductive skew in favour of the dominant pair, they are prime examples to investigate others' motivation to help, although cooperation is largely limited towards pups and for common defence, and food sharing among adults does not exist. This competition for food may explain why so far we have failed to establish a convincing paradigm to test prosociality within a food sharing context (Amici *et al.*, 2017). The first attempts to apply existing methodological



**Table 13.1.** Key aspects relevant to the study of cognition in meerkats.

Key aspect	Natural habitat	Captive groups
Individual marking	Obvious dye marks, transponders	
Get attention to perform experiments	Only when sunning in the morning at sleeping burrow or when resting during the day	During non-feeding periods
Separating from group	Possible for a few minutes, luring away from group with food (e.g. with scorpion on fishing line)	Possible for a few minutes, separating in specific sections of enclosure or experimental cage
Playback experiments	At any time when individuals have emerged	
Habituation to manipulations (e.g. presentations of olfactory or audio stimuli)	Pay attention to context and do not conduct them too often (adjust to natural occurrence rate)	
Observation	If close by, ensure slow and calm movements, never run, make soft calming sounds	If in enclosure, ensure slow and calm movements, observe from outside enclosure or with video
Eye sight	Not very good at close distance, exceptional over far distance (predator recognition)	Not very good at close distance
To calm them down to close presence	Talking to them in soft voice and always move slowly	

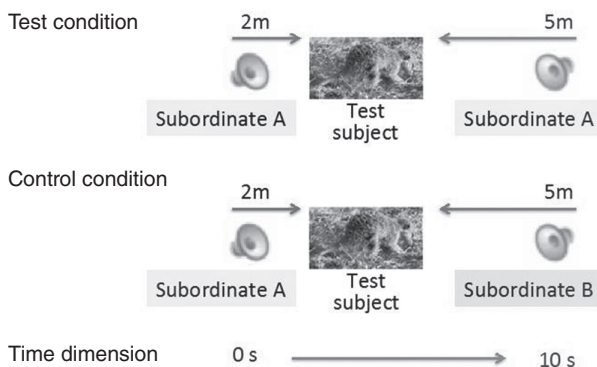
set-ups requiring rope-pulling have failed on meerkats in captivity, as subjects only focused on the food reward, rather than the social partner or the experimental apparatus. Possibly, meerkats cannot pay attention to the environment while suppressing their own motivation to receive food, and end up maximizing their food income, regardless of other group members. Potentially, such an experiment should be repeated when pups are present, to see if they are more prosocial towards pups. As a side note, meerkats usually dig to find their food, so that even when being tested, they may end up digging with their paws, rather than pulling in a goal-directed way. If some pulling mechanism is required, it may be helpful to place it in front of the subjects, so that short-sighted meerkats can realize the presence of such a mechanism due to the contrast.

Meerkats also offer great opportunities to study individually based and social-based learning, as offspring pass through clearly defined phases in their lives. Their first 3 weeks are spent below the ground, with the protection of a babysitter, fully relying on them for food, thermoregulation and protection against predators. Once they emerge to the surface, they are exposed to a very different environment, and they learn the burrow entrance as their safe location, yet they already are exposed to additional ecological stimuli, such as approaching predators when above ground. Finally, as they join the group when foraging, they improve their spatial mapping abilities and have to quickly acquire knowledge on their physical and social environment. Because meerkats do not predominantly use only one sensory modality, but very much rely on acoustical,



olfactory and visual stimuli, they also seem predisposed for tests on how they combine information from different modalities. This is typically done with cross-modal experiments (Proobs *et al.*, 2009), whereby subjects may be primed with information from one modality and then tested to assess whether they can correctly assign the according information from another modality (e.g. testing individual recognition from body odours and relating it to the matching vocalization from that individual). Because loudspeakers and olfactory cues such as faeces can be easily carried to a group, and specific individuals can be tested separately (easiest when the group is stationary at a burrow, but also with slightly more efforts while it forages, see above), such experiments seem feasible.

Other ideal experimental designs to test the knowledge of animals are violation-of-expectation experiments. Here the important point is to understand meerkats' natural behaviour and information processing in a specific situation, and then add the violating context. We have done this in a playback experiment, testing whether meerkats monitor other individuals' spatial location in the group (Townsend *et al.*, 2011). We presented the foraging test subject with a physically impossible situation by simulating the presence of the same group member in two different places within a few seconds, so that it was impossible for a meerkat to move from one place to the other in that time (Figure 13.4). The test subjects responded more strongly to this incongruent situation than during the control, congruent situation (i.e. the physically possible set-up of playing the calls of two different group members at the same two places and after the same time). Such experimental designs are promising to test specific aspects of information processes in situations where test subjects may not typically show a response, although they may have perceived the information (Reber *et al.*, 2013).



**Figure 13.4.** Schematic playback set-up of the violation of expectancy experiment, to test individual discrimination while meerkats are foraging. The test condition represents the incongruent set-up of playing the calls of the same subordinate individual, A, to a foraging test subject, from two different sites and within a short time period. The control condition represents the congruent set-up, in which the calls belonging to two different subordinate individuals A and B were played to the same test subject, from two different sites and within a short time period.

## The Devil is in the Details

### Box 13.2 Communication and Cognition in the Mongoose Family

Alex Thornton

The research described in the current chapter has not only helped to propel meerkats to animal super-stardom, with their fuzzy faces gracing TV screens and billboards around the world, but has also inspired work on other African mongoose species. Although closely related, these species show important ecological and social differences, ranging from solitary (slender mongooses, *Galerella sanguinea*) to facultatively social (yellow mongooses, *Cynctis penicillata*) and cooperative systems that are either despotic (dwarf mongooses, *Helogale parvula*, and meerkats, *Suricata suricatta*) or egalitarian, with all females breeding synchronously (banded mongooses, *Mungos mungo*). These differences provide unique opportunities for comparative research, to understand the selective pressures driving behavioural and cognitive evolution (see Manser *et al.*, 2014). For instance, dwarf mongooses and meerkats use predator-specific alarm calls that elicit different responses, whereas the other species have a less-specific, urgency-based alarm call system. Manser and colleagues (2014) have speculated that differences in escape opportunities, linked to vegetation cover and predator strategies, may determine when functionally referential call systems provide adaptive benefits.

The methodological approaches used to study the different mongooses, including habituation to allow close observation, are broadly similar, but must of course be tailored to suit the requirements of the system. At the most basic level, habitat differences shape the logistics of data collection. In the southern Kalahari, hunting pressure has largely exterminated large predators, so researchers can follow meerkats and yellow and slender mongooses on foot for kilometres, whereas banded mongoose researchers in Uganda never stray too far from a vehicle, in case they need to beat a hasty retreat from assorted hostile megafauna.

On a more fundamental level, knowledge of each species' ecology shapes the design and execution of hypotheses and experiments. For example, Sharpe and colleagues (2013) took advantage of the fact that dwarf mongooses have a linear dominance hierarchy to use playback experiments and show that adults respond differentially to the calls of group members above or below them in rank. Banded mongoose societies are not hierarchical, but they do exhibit a unique form of offspring care in which pups form an exclusive bond with a single adult carer, known as 'escort'. This led Muller and Manser (2008) to hypothesize that escorts and their pups should have means for recognizing one another, and playback experiments suggest that this is in fact the case.

Knowledge of natural history also informs experiments testing animals' knowledge of their physical environments. Meerkats in the sparsely vegetated Kalahari, for example, have exquisite memory of the location of boltholes in their territories, as these provide means of escape from attacking predators (Manser and Bell, 2004).

(cont.)

Banded mongooses, in contrast, tend to dive into bushes when alarmed, but they do seem to remember the locations of hard objects such as rocks and trees, which they use as anvils to crack open encased food items like eggs (McAuliffe and Thornton, 2012). Reports of this behaviour have also led researchers to experimentally test their physical cognition: do mongooses discriminate between hard and soft, and choose anvils accordingly? In short, the answer is no – simple heuristics will do the trick, probably because solid objects in their environment are typically hard (Müller, 2010; McAuliffe and Thornton, 2012).

Truly comparative research remains unfortunately rare in the field of comparative cognition. Research on the mongoose family provides an excellent example of how good old-fashioned natural history can inform the design of elegant and rigorous experiments, to understand the cognitive challenges animals face in their natural environments.

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## Resources

Many film documentaries, including the TV series *Meerkat Manor*, describe the life of meerkats in amazing pictures and with more or less realistic comments about their behaviour. In the BBC documentary *Meerkats: Secrets of an Animal Superstar*, the background of the Kalahari Meerkat Project is presented, illustrating many of the experiments published and discussed above. National Geographic produced a 3D documentary in 2012. The German TV company BR produced two documentaries focusing on Manser's communication work: *Rufe aus der Kalahari* and *Vom Kuscheln, Träumen und Schmusen*. In addition, in many documentaries meerkats appear as short

contributions, e.g. in BBC Earth *Africa*, where the interaction between drongos and meerkats is beautifully shown, based on the scientific publication by Flower and colleagues (Flower, 2011a) (see YouTube BBC drongo meerkat: [www.youtube.com/watch?v=tEYCjJqr21A](http://www.youtube.com/watch?v=tEYCjJqr21A)). The first documentary to make the meerkats famous was that by the BBC, called *Meerkat United* (1987).

The website of the Kalahari Research Centre provides much information on the species and also on the project and the habitat where meerkats occur. It also lists all the scientific publications and popular contributions (<http://kalahari-meerkats.com/kmp/>).

In a book written for the public with the same title as the TV series *Meerkat Manor*, Clutton-Brock (2010) describes the findings of our research over the first 10 years of the project, and gives a good introduction to the lives of meerkats for a popular audience. There are also several articles in popular science magazines (Milius, 2007) and on the Internet, such as a recent National Geographic blog ‘Meerkats mysteriously know to outgrow rivals’ (<http://phenomena.nationalgeographic.com/2016/05/25/meerkats-adjust-their-growth-to-match-their-rivals/>).

## Profile

Marta’s interest in meerkats began with her PhD under Tim Clutton-Brock’s supervision on the evolution of vocal communication. Tim Clutton-Brock (Cambridge University, UK) founded the long-term Kalahari Meerkat Project, to investigate cooperative breeding in mammals. During Marta’s PhD, it became obvious that meerkats coordinate their activities in similar ways to that described by Cheney and Seyfarth (1992) on vervet monkeys. Her research was very much influenced by a similar approach on understanding the function of alarm, contact and pup begging calls. During Marta’s post-doc and in her later group leader positions, she became more interested in also trying to take into account meerkats’ knowledge of their social and physical environment. The research of her group currently focuses on function and mechanisms of vocal and olfactory communication, collective behaviour, group decision-making and group movement. They are also investigating physiological aspects of vocal production and perception.

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