



Spatial representation of shelter locations in meerkats, *Suricata suricatta*

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We used observations and manipulation experiments to investigate how meerkats, social mongooses living under high predation pressure, find shelter from predators quickly within their territory. We played back alarm calls to foraging meerkats and dug new boltholes and covered existing ones to see whether location or other cues were used. Meerkats almost always ran to the bolthole closest to them. This was not done by a simple rule of running back to a bolthole they had just passed, nor by escaping in any direction and finding a bolthole by chance. Meerkats nearly always ignored the boltholes that we dug but ran to those we had covered up. Our results support the hypothesis that meerkats know in which direction to run when an alarm call is given, without scanning the area for visual or olfactory cues of shelters. As meerkats have more than 1000 boltholes in their territory, our results suggest that they have detailed knowledge of the direction and the distance of specific locations. However, this does not necessarily mean that they have a spatial map of their territory; our results may be explained by place recognition or reorientation of specific landmark features.

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From insects (Müller & Wehner 1988; Dyer 1994) to fish (Sovrano et al. 2002), birds (Kamil et al. 1994) and mammals (Etienne et al. 1996), we find species that show impressive navigational skills. Such behaviour has been investigated in the context of how animals find their way around their home ranges (e.g. Menzel 1997; Janson 1998), retrieve knowledge about the location of stored food (Kamil et al. 1994), and, to a lesser extent, find shelter (reviewed in Shettleworth 1998). The question has arisen whether animals represent spatial information internally by using a spatial (or cognitive) map, similar to that suggested for humans (Wang & Spelke 2002). In general, such internal representations reflect the ways in which information is obtained by the senses, translated, processed and encoded in the brain into a format that reconstructs a view of salient features of the environment (Real 1994). Some authors have used the term cognitive map to describe any form of spatial representation maintained by an individual (e.g. Gallistel 1990). In contrast, Tolman (1948) and O'Keefe & Nadel (1978) restricted the use of this term to the ability to construct mentally a map

of large-scale space in which landmarks are represented within a common coordinate system. In this type of cognitive map, also called a Euclidean map, the actual positions of landmarks and other features of the environment are geometrically represented as true angles and distance relationships (Bennett 1996). This would require the ability to reorient, integrate and reconstruct large numbers of individual local views of places and landmarks in the environment into a single geometric 'global-view-from-above' of large-scale space (Benhamou 1996).

Some authors have questioned whether animals can truly represent spatial information in such a detailed way to perform 'global' place navigation, and have pointed out that this has never been demonstrated or properly tested (Poucet 1993; Benhamou 1996; Garber 2000). Wang & Spelke (2002) pointed out that human navigation might not depend on internalized versions of geographical maps, but rather be based on similar mechanisms to those previously described in animal navigation, such as path integration, place recognition and reorientation. Animals relying on path integration continuously update vectors describing their distance and direction to one or more significant locations, called egocentric positions, as they move (Müller & Wehner 1988). Animals using place recognition appear to form snapshot views so that the visual image of the environment is about the same each

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time an animal approaches the specified location (Cartwright & Collett 1983; Dyer 1994, 1996). Reorientation in fish, birds and mammals is primarily based on geometric features of their environment (Cheng 1986), but can also be influenced by nongeometric characteristics (Suzuki et al. 1980; Cheng & Spetch 1998; Save et al. 1998).

We investigated spatial representation and potential mechanisms that could explain knowledge of shelter locations in a species living under high predation pressure. For animals with frequent predator encounters and large home ranges, it is advantageous to know the location of the closest shelter to reduce the length of the escape route, and therefore the likelihood of being caught by predators. In particular, for species whose predators approach unexpectedly at high speed, knowing immediately where to find the closest shelter will be crucial for survival. Natural selection in such species will therefore not only have favoured the evolution of highly efficient ways of escape, but also have selected for individuals with specific knowledge about the locations of shelters.

Meerkats, cooperatively breeding mongooses, occupy large territories of about 2–4 km² with 5–20 sleeping burrows that typically have several entrances (T. Clutton-Brock, unpublished data). Groups of 2–45 members travel as a cohesive unit from burrow system to burrow system and renovate boltholes on their way, which they use as shelters when a predator alarm is given. Meerkats live in semidesert open areas and dig for their prey in the sand. They frequently encounter aerial and terrestrial predators, and have to interrupt their foraging to find shelter about every 40 min (Manser 2001). The response to aerial predators has to be immediate and each group member benefits by finding the closest shelter to its current position, independently of what the other group members are doing.

Four strategies could explain the meerkats' success in finding shelter immediately when an alarm call is given. First, meerkats may always run back to the last bolthole they passed while foraging. Second, meerkats may have an exact knowledge of their own position relative to the shelter locations within their territory, and always run to the bolthole closest to them. Third, meerkats may use visual or olfactory cues to find the closest bolthole. Fourth, meerkats may choose any direction and, because of the large number of boltholes available in their territory, they run into one after a short distance or time. To test these four hypotheses we used observations on foraging meerkats responding to predator alarm calls of other group members. We also performed manipulation experiments, by playing back alarm calls, and we dug new boltholes and covered existing boltholes in a group's territory to investigate whether meerkats use the location of boltholes or visual and olfactory cues to find them.

METHODS

We collected data from January to August 1999, June to December 2000 and February to April 2002 on a wild population of meerkats on a ranch in the southern part of the Kalahari, 30 km west of Van Zylsrus, South Africa (Clutton-Brock et al. 1998). The study was conducted under permission of the Northern Cape Conservation

Service, South Africa. We followed 10 groups with a total of 123 adult individuals along the dry riverbed of the Kuruman. All individuals were easy to identify by natural marks or specific patches on the body, where we cut their hair. These marks were kept small and applied without disturbing the animals while they were sunning in the morning. They were habituated to a degree that allowed us to follow them within 0.5 m.

Shelter Availability and Its Use

We estimated the number of potential shelters in a territory, by counting in an area of 100 × 100 m all the foraging holes larger than 60 cm long (holes dug out but not renovated) and boltholes (holes that had been obviously renovated), the number of burrow entrances per burrow system, and any other obvious shelter, such as tree trunks, dead trees and piles of branches. We did this on six territories, in three habitats per territory: (1) riverbed; (2) flat area (other than riverbed); (3) slope dune area.

Meerkats mainly use boltholes as shelter when alarm calls are given, and they almost never use a foraging hole (personal observation). We therefore concentrated the analysis of shelter use on the boltholes. To understand how meerkats used boltholes, we documented their behaviour when they passed within 5 m of a bolthole. We examined: (1) whether meerkats passed by and ignored it; (2) whether they inspected it by sniffing around and going below; and (3) whether they renovated it by digging out sand. We also investigated how often a bolthole was used in response to an alarm call, and we also measured the distance from one bolthole to the next.

Which Boltholes are used?

To test whether meerkats have an accurate knowledge of the bolthole locations in their territory, or whether they use a simple rule always to run back to the last bolthole they had just passed, we recorded to which bolthole an individual ran during naturally occurring predator encounters. We focused on one subject during foraging and followed it until a predator alarm made it run to a bolthole. We then noted whether it ran forward to a bolthole it had not passed during the last 15 min or whether it ran back to one passed earlier. We also estimated the distance and time it took a meerkat to run to a bolthole from the moment the alarm call occurred. We checked whether the chosen bolthole was the closest one to where the subject had been foraging at the time of the alarm call, by estimating the distance of all the boltholes nearby. We collected these data for 100 adults, each time a different individual ($\bar{X} \pm \text{SD} = 2.4 \pm 1.1$ years old, range 1–5) in 10 groups when an aerial alarm call was given and the target individual ran to a bolthole for shelter.

More experienced animals in the group may have a more accurate knowledge about locations in their territory. Therefore, we tested whether age, status or sex had an effect on the escape behaviour and the way of finding shelter. Birth dates were known for all individuals in the study. We included only adult animals older than 1 year. To test whether older, more experienced animals were

more likely to run to the closest bolthole, we divided the age into 1-year periods (from 1 to 5 years). Dominant individuals were identified by their behaviour, in particular marking frequency (T. H. Clutton-Brock, unpublished data), and were usually the ones breeding (Clutton-Brock et al. 2001).

Playback experiments

In addition to observations we used playback experiments to find out to which boltholes meerkats were running, and what kind of cues they might use from the environment to find them. We played an aerial alarm call of medium urgency (for a description see Manser 2001) to make them run for shelter. We performed this three times in six groups, each playback on a different individual.

For the playback experiments we used high-quality calls (10 different examples) recorded with a directional Sennheiser microphone MKH 816 and a digital audio tape (DAT) Walkman recorder Sony PCM-M1 (see also Manser 2001). We edited the calls using Canary 1.2.1 software (Bioacoustic Laboratory, University of Cornell, Ithaca, NY, U.S.A.) on a MacIntosh Powerbook G3-series. The calls were then played back with a DAT Walkman connected to a Sony Walkman loudspeaker SR A60. Call amplitude was adjusted to what we had observed during naturally occurring alarm calls. Playbacks were conducted only on foraging groups and when the subject was at least 10 m from the closest bolthole. We did not play a call if there had been an alarm call or another disturbance that had caused the group to run to a bolthole within the last 15 min. We recorded the response of the subject to the alarm call, describing whether it first scanned the area or ran immediately for shelter, and to which bolthole it ran. Typically, we conducted only one playback per week in the same group.

Do Meerkats Use Visual or Olfactory Cues?

Test for visual cues

To test whether meerkats rely on visual cues, we dug new boltholes to see how likely meerkats were to go over and use them. We kept digging boltholes with six groups until we had two successful attempts per group in that at least one of the meerkats passed within 10 m of the new bolthole. We considered only these observations in the analysis.

To investigate whether meerkats that respond immediately to an alarm call run to the closest bolthole they can see, we played calls to subjects that were within 10 m of the new bolthole. We placed the playback equipment about 20 m from the new bolthole in the direction the group was most likely to move while foraging. We waited until a meerkat was 10–20 m from the new bolthole and the loudspeaker to play the alarm call. If meerkats were using visual cues to find the closest place that looked like a bolthole, they should have run to these new boltholes. If they ran to one of the other boltholes, it would indicate that they went there because they knew exactly where to go.

Test for location and olfactory cues

Since meerkats not only used boltholes for shelter, but also renovated them frequently as they passed by on their

foraging route, we tested whether they had an expectation of finding a bolthole at a specific location. We therefore covered boltholes (with car floor mats and sand on top) ahead of the foraging group and made the spot look like the surrounding sand area. If meerkats had an expectation of finding boltholes at specific positions, we predicted that they would go over and investigate the area. Furthermore, because meerkats seemed to investigate and renovate large boltholes any time they passed close by, whereas they frequently ignored smaller boltholes, we covered one large bolthole and one small bolthole in each of six groups' territories. Large boltholes were defined as those that had been renovated several times before and the dug-out area was more than 0.5 m; small boltholes had been rarely renovated and the dug-out area was less than 0.5 m. We recorded whether an individual that passed within 10 m of such a covered bolthole would go over and sniff around or try to dig at the original place of the bolthole.

We also tested responses to alarm calls by playing the call to a subject within 10 m of a covered bolthole at its original location. We recorded whether they would still run over to these locations, and how they responded when they could no longer find the bolthole. We performed this experiment on subjects in six groups. We conducted playbacks only when no predators had been seen in the area for the previous 30 min. In no case did a predator approach during the experiment.

The original covered boltholes might have attracted meerkats to inspect them because of their smell from meerkats that had recently used them. To ensure that the location, and not olfactory cues, was the reason the meerkats might run to a specific location, we dug up the sand and flattened it again in places where no boltholes existed before. In addition, to simulate the smell of a recently used bolthole, we used sand from the sleeping burrow that had been renovated and marked by the group that morning. We again recorded in six groups whether an individual that passed within 10 m of such a location went over to investigate it.

Similar to the above set-up, we tested the response to alarm calls with a covered bolthole with olfactory cues at a place where no bolthole existed before. We conducted playbacks with subjects in six groups that passed such a spot within 10 m. If meerkats were using olfactory cues to find the closest shelter, they should have run to these spots. If they escaped to one of the other boltholes, it would support the hypothesis that they ran to a bolthole the location of which they had memorized.

RESULTS

Shelter Availability and Its Use

On average, we counted in an area of 100×100 m ($N = 6$) a mean \pm SD of 5.0 ± 7.0 foraging holes, 7.2 ± 5.2 boltholes, 0.6 ± 0.9 burrow systems with 2.8 ± 2.4 burrow entrances and 5.8 ± 10.3 other potential shelters, such as tree trunks, dead trees or piles of branches. There was no significant difference between the three habitats investigated (Friedman: $\chi^2_2 = 2.8$, $N = 5$, $P = 0.25$) although there was a tendency for more boltholes to be

found in the riverbed and in flat areas than in dune areas (Table 1). Extrapolating the number of boltholes from the count in an area of 100×100 m to the average territory size of 2.99 ± 0.77 km² ($N = 6$) suggests that meerkats could encounter 2157 ± 793 boltholes within their territory.

The average distance between boltholes that the meerkats passed nearby, walked over, renovated or used as shelter after an alarm call \pm SD was 46.4 ± 13.3 m ($N = 6$ groups), which meant that one or more individuals encountered a new bolthole every 9 ± 3.5 min while foraging. Of these boltholes $23 \pm 5.7\%$ were not investigated at all, $37 \pm 7.8\%$ were inspected briefly, $32 \pm 3.2\%$ were renovated and $24 \pm 6.2\%$ were used as shelter after an alarm call.

Which Boltholes are Used?

In 100 events of aerial alarm calls, meerkats ran to the bolthole they had just passed in 40% of cases and to one they had not passed by during that foraging session in 60% of cases (Table 2). In 83% of cases they ran to the closest one (binomial two-tailed: $P < 0.001$). The average estimated distance in their escapes to aerial alarm calls \pm SD was 28 ± 12.8 m ($N = 6$ groups), with an average escape time \pm SD of 5.8 ± 4.5 s. They never had to run further than 60 m to find a bolthole.

Of the 18 playbacks of alarm calls that caused the meerkats to run to a bolthole, in 72% of cases they went to a bolthole not passed while foraging (Table 2). In these cases they usually (77% of cases) ran to the bolthole closest to their foraging position in any direction. In four of the five cases when they ran back to a bolthole, it was the closest one (Table 2). Therefore, in 14 of the 18 (78%) playbacks, the meerkats ran to the closest bolthole (binomial two-tailed test: $P < 0.05$).

Age, status and sex did not have a significant effect on escape behaviour (age: Spearman correlation: $r_s = 0.5$, $N = 5$, $P = 0.29$; status: Wilcoxon signed-ranks test: $T = 17$, $N = 10$, $P = 0.51$; sex: Wilcoxon signed-ranks test: $T = 9$, $N = 10$, $P = 0.21$).

Do Meerkats use Visual or Olfactory Cues?

Test for visual cues

In the trials where we dug new boltholes and at least one meerkat passed within 10 m of it when foraging, in

Table 1. Number of shelters per 100 m² ($\bar{X} \pm$ SD) in three habitat types in six territories (except for one territory that did not have any riverbed area)

Type of shelter	Dune	Flat areas	Riverbed
Foraging holes	2 ± 2.8	12.2 ± 10.5	0.6 ± 0.6
Boltholes	4.3 ± 2.8	8.2 ± 4.6	10.2 ± 6.9
Sleeping burrows	1.1 ± 1.1	0.8 ± 0.8	1.2 ± 0.8
Entrances per sleeping burrow	3.1 ± 3	2.5 ± 2.5	2.6 ± 1.7
Other shelters*	13.8 ± 13.2	0.5 ± 0.6	1 ± 0.7

*These include tree trunks, dead trees and piles of branches.

only 25% of cases did one of them go over to inspect it (binomial two-tailed: $P = 0.15$; Table 3). In two cases, only one meerkat went to investigate it, and they lost interest within 10 s. In the third case, one of them began to dig and two other meerkats nearby came over and joined it.

In the 12 playbacks, the meerkats usually ran to other boltholes and ignored the new one (binomial two-tailed: $P < 0.01$; Table 3). In 10 cases (83%), the new bolthole was the closest one to the foraging meerkat at the moment the alarm call was played back.

Test for location and olfactory cues

When meerkats passed within 10 m of an area where we had covered the original boltholes, in 75% of cases (binomial two-tailed: $P = 0.15$; Table 3) they went over and either sniffed around, or began to dig. They showed interest in all six large boltholes but only three of the six small ones (Fisher's exact test: $P = 0.18$; Table 3).

In the six playbacks with covered boltholes at their original location, the meerkats ran to them in 83% of cases (binomial two-tailed: $P = 0.21$; Table 3). In one case, the cover fell through after a few seconds of the meerkats digging and trying to get in. They continued to renovate the bolthole for about 5 min and then resumed foraging. In two cases they ran to the next bolthole 5–30 m away, and in the other two cases they just ran to the next pile of branches and then relaxed.

In 25% of tests on olfactory cues (binomial two-tailed: $P = 0.15$; Table 3) a meerkat passing within 10 m went over to the manipulated location. In two of these cases they just smelled it, and in one case an individual began to dig, but lost interest after about 10 s.

In the playbacks, none of the subjects (binomial two-tailed: $P < 0.05$) ran to the spot that looked like a covered bolthole and smelled it (Table 3).

DISCUSSION

Adult meerkats appeared to know exactly where they were within their territory, and in relation to specific features. Observations and manipulation experiments showed that they knew where to run for shelter, independent of where they were in their home range. They did not use simple rules to run for shelter, nor did they use visual or olfactory cues. Rather, they seemed to have an accurate knowledge of the distance and direction to the closest shelter in relation to their own position in their territory at any time.

Meerkat territories had more than several thousand boltholes that they could use for shelter, which is a substantial number of exact locations to remember. Nevertheless, as observations and experiments showed, meerkats did not just always run to the bolthole they had last passed. They more often ran to a bolthole they had not seen during that foraging session. The probability that they ran by chance in one direction and finally found a bolthole is unlikely. Meerkats usually ran to the closest bolthole. Typically, their escape lasted only a few seconds, and the average distance to a bolthole was less than 30 m and never further than 60 m. If they were running in

Table 2. Boltholes used for shelter after an alarm call depending on whether the meerkats had just passed them or whether they were the closest to their current position when the call occurred

	N	No. of groups	No. of subjects tested	Bolthole just passed		Bolthole not just passed	
				Closest	Not closest	Closest	Not closest
Observations	100	10	100	33	7	50	10
Playbacks	18	6	18	4	1	10	3

Data are from observations and playback experiments.

random directions and finding boltholes by chance, one would expect more variation in escape times and distances. In particular, meerkats would sometimes be expected to run much further than only 60 m considering that the average distance between boltholes was 46 m.

Meerkats did not use visual or olfactory cues to find the closest shelter. Instead of looking around for boltholes, they ran to them in more or less a straight line without scanning the surroundings. Often they were not able to see the bolthole from their foraging position at the time the alarm call was given. That meerkats do not depend on visual or olfactory cues to find boltholes was also confirmed by the experiments where we dug out new boltholes, or covered existing boltholes, and tested whether they would walk to those areas and inspect them. Furthermore, meerkats appeared to be able to orient themselves from any angle. When hearing an alarm call they never had to orient themselves first and then turn around; they always ran immediately in the right direction.

Occasionally meerkats did not run to the closest bolthole, which suggests that they did not know the location of all of the boltholes available. When testing whether more experienced group members were more likely to escape to the closest shelter, we did not find obvious evidence that older individuals ran more often to the closest boltholes. Status and sex also did not explain the likeli-

hood of finding the closest bolthole. The manipulation experiment showing that areas of formerly large boltholes were used more often than the locations of formerly small boltholes supports the hypothesis that meerkats have a selective knowledge of specific boltholes. Other reasons, such as the direction of the centre of the group relative to boltholes, or whether a direct escape route from the foraging position to the bolthole was not possible, could also be important. Nevertheless, meerkats still appeared to know a large proportion of the boltholes available in their territory, which still leaves several hundred or more locations to remember. This ability to memorize many locations might be comparable to the skills of food-storing birds (Shettleworth & Krebs 1986).

What mechanism might explain the knowledge that meerkats have about their own position relative to the location of a large number of boltholes in their territory? We can exclude path integration (Müller & Wehner 1988), where animals continuously update their position to a specific location (egocentric position). Path integration could apply if meerkats had always run to the boltholes that they had just passed, updating each bolthole as their new egocentric point. However, since they often ran to the closest bolthole they had not passed, this can be excluded. It is more difficult to distinguish between other spatial module concepts, including place recognition, reorientation, or a spatial map, with the existing data. Meerkats might have specific foraging routes along which they learn the different boltholes, similar to what has been described for bees. In this case, meerkats might compare memorized 'snapshot views' to recognize a place (Cartwright & Collett 1983; Dyer 1994, 1996), or use specific landmark features for reorientation of small areas within their territory (Cheng & Spetch 1998; Save et al. 1998). Both mechanisms, place recognition and reorientation, might be enough for them to orient themselves to one of the closest boltholes at any time, without relying on visual or olfactory cues while foraging. Thus, the accurate knowledge meerkats have about directions and distances does not necessarily mean that they have a representation of a Euclidean map (Tolman 1948; O'Keefe & Nadel 1978). Rather than reconstructing local views of boltholes in relation to other features in the environment into a single geometric 'global-view-from-above' of large-scale space (Benhamou 1996), meerkats may simply update their present local view of the environment either by place recognition or by reorientation. This does not diminish their remarkable skills in comparing the distance

Table 3. Proportion of manipulated boltholes (newly dug, covered, or newly dug and covered again) that were inspected or ignored by meerkats when they passed close by (observations), or when an alarm call was played to make them run to the closest shelter (playbacks)

Hypothesis	Bolthole size	Data from	Ignored	Used (%)
Visual cues		Observations	9	3 (25)
		Playbacks	11	1 (8)
Location & olfactory cues	Large	Observations	0	6 (100)
		Observations	3	3 (50)
	Small	Playbacks	1	5 (83)
		Playbacks	6	0 (0)
Olfactory cues		Observations	9	3 (25)
		Playbacks	6	0 (0)

Hypotheses: if meerkats use visual cues to find boltholes, they should run to newly dug boltholes; if they use location and olfactory cues, they should run to covered boltholes with olfactory cues of boltholes present at their original location; if they use only olfactory cues, they should run to newly dug boltholes that had been covered again and that had olfactory cues of boltholes.

and direction of specific features in their home range at any time or location. It suggests that navigation based on momentary and egocentric rather than geocentric representations allows animals to locate themselves in relation to specific features even in rather complex environments.

The evolution of the ability to gain and retrieve information on a large number of locations is not too surprising considering the high predation pressure that meerkats experience in their habitat (Clutton-Brock et al. 1999; Manser 2001). It will be difficult to determine what features meerkats use to orient themselves, as it is almost impossible to manipulate landmarks in the environment in which they live. However, by studying their home range use in more detail, we may find that meerkats use specific foraging routes. A more detailed analysis, of why meerkats ran in a quarter of all cases to a more distant shelter may help us to understand the spatial representation of the meerkats. For example, meerkats may take not only the distance into account, but also the time needed to reach the bolthole. Depending on whether they can reach a bolthole in a direct way, or whether they have to run around an obstacle, they may choose a bolthole further away, because this escape route is less time consuming. Or a meerkat at the edge of the group may choose to run to a place towards the centre of the group, rather than away from it, so as not to lose contact with the other group members. Furthermore, by investigating the development of the ability to choose the closest bolthole in response to predator alarm calls, we may better understand how meerkats learn to memorize the locations of several thousand boltholes within their territory.

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