MASTERARBEIT / MASTER'S THESIS

Titel der Masterarbeit / Title of the Master's Thesis

"Sentinel behaviour of captive meerkats

(*Suricata suricatta*)"

verfasst von / submitted by

Florian Dominik Hüls, BSc.

angestrebter akademischer Grad / in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien, 2019 / Vienna 2019

Studienkennzahl lt. Studienblatt / degree programme code as it appears on the student record sheet:	UA 066 831
Studienrichtung lt. Studienblatt / degree programme as it appears on the student record sheet:	Masterstudium Zoologie
Betreut von / Supervisor:	Mag. Dr. Angela Stöger-Horwath, Privatdoz.

Eidesstattliche Versicherung

Hüls, Florian

Ich erkläre hiermit an Eides statt,
dass ich die vorliegende Masterarbeit mit dem Thema

„Sentinel behaviour of captive meerkats”

selbstständig verfasst, mich außer der angegebenen keiner weiteren Hilfsmittel bedient und alle Erkenntnisse, die aus dem Schrifttum ganz oder annähernd übernommen sind, als solche kenntlich gemacht und nach ihrer Herkunft unter Bezeichnung der Fundstelle einzeln nachgewiesen habe.

Wien,

Florian Hüls

Danksagung

An dieser Stelle möchte ich mich bei all denjenigen bedanken, die mich während der Anfertigung dieser Masterarbeit unterstützt haben.

Zuallererst möchte ich mich bei Frau Dr. Angela Stöger bedanken, die meine Masterarbeit betreut und begutachtet hat. Für die hilfreichen Anregungen und die konstruktive Kritik bei der Erstellung dieser Arbeit möchte ich mich herzlich bedanken.

Vielen Dank auch an meine Prüfer Herrn Professor Kratochvil und Herrn Professor Krenn.

Des Weiteren möchte ich mich bei meinen Ansprechpartnern bzw. den Verantwortlichen der drei Zoos recht herzlich bedanken. Vielen Dank an Dr. Martina Heiderer (Tiergarten Schönbrunn), Dr. Barbara Jantschke (Zoo Augsburg) und Elisabeth Hölzl (Zoo Linz) für die Mithilfe und die Möglichkeit, meine Masterarbeit in den jeweiligen Zoos durchführen zu dürfen.

Bedanken möchte ich mich auch bei den zuständigen Reviertierpflegern der jeweiligen Zoos in Wien, Augsburg und Linz, die mich mit vielen wichtigen Informationen zu ihren Tieren versorgt haben und die jederzeit für meine Fragen offen waren.

Auch bei meinen Kommilitonen Britta, Tim und Hannah möchte ich mich bedanken. Ihr habt dafür gesorgt, dass ich zwischendurch auch mal abschalten und auf andere Gedanken kommen konnte. Danke dafür.

Zum Schluss möchte ich mich vor allem bei meiner Familie bedanken. Bei meinen Eltern, die mir mein Studium durch ihre Unterstützung ermöglicht haben und immer ein offenes Ohr für mich hatten und bei meinen beiden Schwestern, die mir zu jeder Zeit mit Rat und Tat zur Seite standen. Mama, Papa, Corinna und Julia, vielen Dank für eure Unterstützung! Ihr seid die Besten!

Florian Hüls

Wien, Juli 2019

Table of contents

1 Abstract

Meerkats are well known and popular for their distinct social life and cooperative behaviour. The sentinel job in meerkats represents a responsible task within the group, raising the question whether certain individuals in a group are more suitable as a sentinel than others. This study examines the behaviour of captive meerkats during guard's work, focussing on individual sentinels in detail as well as on group performance. Several sequences of sentinel behaviour of meerkat groups in three different zoos were recorded. These were analysed in detailly regarding the duration of single guarding sequences, the guard poses taken and the guard positions of the individuals. A second focus was on the reaction of the responsible sentinel and the whole group to various bird calls. Finally, I investigated the existence of so-called 'super sentinels' in meerkat groups as well as individual preferences of sentinels. The results demonstrated that certain individuals do the guard job more often and even more effectively than other group members. The sentinels preferred elevated spots for their work and the taken guard pose differed between the meerkat groups. It became clear that the groups had at least one guard on duty most of the time and that the periods without any guard were very short. The playback sequences of predatory bird or songbird calls revealed major differences between the investigated meerkat groups. Some calls of certain bird species induced stronger reactions than others, and the sentinels showed that meerkats are able to categorize other species as potentially dangerous or harmless. The observations yielded information on the required characteristics of a 'good' sentinel and indicated other parameters such as group size and enclosure area that may influence the guard work. This investigation showed that the sentinel behaviour of captive meerkats is very similar to that of their conspecifics in the wild. The reaction to possible predators by the sentinels is affected by the sentinel's character, by past experience and the presence of offspring within the group.

2 Introduction

In the animal kingdom, sentinel behaviour, also known as guarding behaviour, is a special form of altruism in cooperative societies (Ridley, Raihani, & Bell, 2010). Sentinel behaviour has been described in various species, best known for example in mammals such as marmots, mongooses and prairie dogs but also in different bird species such as the pied babbler (Ridley, Nelson-Flower, & Thompson, 2013). A common assumption is that sentinel behaviour functions to provide benefits in terms of increased predator detection. The detection of predators is generally dependent on group size, with smaller groups suffering higher mortality rates than larger groups (Clutton-Brock et al., 1999b). This makes the installation of guards helpful and is often observed in animals that forage in groups. Sentinel behaviour allows the individuals to reduce their own vigilance while maintaining the alertness of the group. This behaviour is characterized by two main points: (1) certain individuals of the group scan for predators while the rest of the group pursue other activities (e.g. foraging) and (2) the sentinel(s) are usually on duty in elevated positions to ensure a good look-out over the environment (Ridley et al., 2013). Meerkats are one of the most popular examples for sentinel behaviour because of their characteristic and unique pose standing erect on the hind legs.

Despite the still inconclusive evidence on the mechanisms (costs and benefits), sentinel behaviour can be designated as a very successful example for evolution. There are two contrary hypotheses regarding the evolution of sentinel behaviour. The first hypothesis describes it as cooperative, altruistic behaviour in which the group members benefit from the sentinels and their early detection of possible predators. The second hypothesis refers to a selfish behaviour because the sentinels have the chance to escape early after detecting enemies and individual safety has priority (Ridley et al., 2013).

In any case, sentinel behaviour is clearly helpful to survive and an important strategy for various animal species to protect the group against predators, whereby cooperation within groups is decisive.

Figure 1: Slender-tailed meerkat (Suricata suricatta)
Classification: Class Mammalia; Order Carnivora; Suborder Feliformia; Family Herpestidae;
Conservation status: IUCN Red List: population trend stable; Least Concern (2015).

2.1 Altruism in meerkats

Meerkats (*Suricata suricatta,* Schreber, 1776) (Figure 1) are often used as model organisms for altruistic behaviour due to their cooperative breeding and feeding as well as community guarding. Meerkats are strictly diurnal, terrestrial mammals. They occur in southern Africa (Angola, Namibia, Botswana, South Africa) and their natural habitats are shrubland, savanna, grasslands and desert areas (Von Staaden, 1994). Meerkats occupy territories that may extend for several square kilometres and encompass dozens of overnight burrows and hideouts (Ross-Gillespie & Griffin, 2007). *Suricata suricatta* belongs to the smallest representatives of the mongoose family (Wilson & Mittermeier, 2009). In their natural habitats, meerkats rarely become older than 8 years because of high predation risk. Each group member forages individually, but the animals always maintain visual and vocal contact like most social mongooses (Estes, 2012).

Meerkats fear various potential predatory species. The most feared predators come from above, i.e. several birds of prey including eagles, buzzards or hawks. Further predators are all larger terrestrial carnivores such as jackals, wild dogs and snakes. Most snakes, however, are potentially dangerous only for the juveniles because adult meerkats are immune to high doses of snake toxins, tolerating up to six times more than a rabbit (Dennis & MacDonald, 1999). Healthy meerkat groups can compensate a certain mortality rate when the birth rate within the group is high enough to enable regeneration. Nonetheless, in years of food shortage the annual mortality rate increases and about the half of the adult animals become predator victims (Clutton-Brock et al., 1999b). Because they lack of good running, climbing and jumping abilities and prefer open habitats, meerkats have evolved several anti-predator strategies such as alarm calls, high-sit alert stance, flight to cover, defensive threat, mobbing attack, self-defense and covering young (Estes, 2012).

A typical meerkat group in the wild consists of about 10 individuals, but groups with up to 30 members are not uncommon. Each group has a dominant pair with an α-female as the leader of the group and an α-male. Reproduction is monopolised by a dominant pair of breeders and their progeny represents about 75% of the group’s offspring. Based on the cooperative breeding system, the alpha female is able to breed multiple times per year, yielding up to 3 litters with 3 pups each in average (O’Riain et al., 2000). Whereas the breeding season in the wild is during the warmer, rainier period from October to April, meerkats in captivity breed year-round (Estes, 2012). Additional group members consist of a variable number of helpers of both sexes and are often relatives of the dominant female. Sometimes, however, other unrelated immigrant individuals (mostly males) are integrated as well (Dennis & MacDonald, 1999) (Clutton-Brock et al., 1999a, Clutton-Brock, 2002) (Clutton-Brock et al., 1999b).

The cooperation between individuals within meerkat groups is one of the most interesting behavioural patterns regarding group living in social animals. The fact that some individuals show altruistic characteristics to gain benefits for the whole group or other individuals is one reason why meerkats are so often the subject of behavioural research. Except for pups under the age of 3 months, all group members show cooperative behaviour such as baby-sitting, pup feeding, social digging and raised guarding (Tatalovic, 2010). Nonetheless, individual and sex-dependent differences in cooperative behaviour are evident between the individuals within one group regarding the time they spend on doing each of these cooperative altruistic acts (Clutton-Brock, 2002).

The altruistic behaviour of some individuals yields benefits for other group members. At the same time, early recognition of potential predators by guards or the help with raising non-related offspring can also involve higher costs. Altruistic individuals consume more energy and have less time for foraging or are exposed to a higher risk of predator attacks (Zahavi & Zahavi, 1997). Despite these caveats, cooperation behaviour is one of the recipes for the success of meerkats. These animals are an excellent model system to test hypotheses arising from the theory of evolution because the existence of altruistic behaviour in humans and animals is one of the major unresolved issues in evolutionary biology (Tatalovic, 2008).

2.2 Sentinel behaviour in meerkats

The sentinel behaviour of meerkats has often been the subject of studies in behavioural research. Especially the research groups of Clutton-Brock and Manser dealt more precisely with the behaviour of meerkats during guarding sequences, providing a major contribution to today's state of knowledge about this animal.

The main defensive strategies of meerkats against predators are sentinel behaviour and alarm calls. Meerkats are famed for their guard work and for having individuals on duty as sentinels. Some studies showed that established guards call out different alarms depending on the different types of approaching predators (Manser, 1999; Manser et al., 2001; Manser et al., 2002). Moreover, the alarm calls signal the urgency of the threat (Manser et al., 2002).

Meerkat sentinels scan the horizon from an elevated position, and their excellent depth perception helps them to detect enemies at great distances. While the guard is on duty, it constantly gives a signal termed 'watchman's song'. This regular vocalization maintains the contact between sentinel and group, announcing that there is no current danger. As a result, the optimum level of vigilance of each group member decreases, enabling them to carry out other tasks such as foraging without interruption (Manser, 1999)(Tatalovic, 2010).

The fact that meerkats position guards on elevated positions (Clutton-Brock et al., 1999a) and that they have specific calls for specific predator classes (Manser et al., 2002) supports the theory that the alarm call signals the predator that it has been discovered by the guard. Thus, the approaching enemy knows it has been spotted and that its chances of success are gone.

Hollén and Manser (2007) showed that the alarm call patterns of wild meerkats were also present in captive-born meerkats in broadly similar contexts. Furthermore, that authors showed that captive meerkats with no prior experience with odours of potential predators were able to distinguish between faeces of carnivores and herbivores (Hollén & Manser, 2007). Accordingly, meerkats show inherent anti-predator behaviour and can detect potential danger without having acquired significant experience in their natural habitat. Moreover, meerkats always approach the nearest hideout when potential danger appears, even if they cannot see it. Their outstanding orientation capability and memory means they always know where to find the nearest shelter (Manser & Bell, 2004).

Importantly, guarding behaviour is beneficial not only for the rest of the group. The guard itself can benefit as well because, as a successful sentinel, it gains prestige and a better status within the group by demonstrating its quality as a mating partner, group member or a rival capable of reliable guarding work (Zahavi & Zahavi, 1997).

Within wild meerkat groups, some individuals do guard work more often than others, are on duty for longer time periods, and spot from higher positions. These so-called ‘super sentinels’ are more vigilant than others: they even interrupt their other activities to check for potential predators when they are not on duty. This was explained by higher levels of the stress hormone cortisol (Tatalovic, 2008). Against expectation, super sentinels are usually well-fed, indicating that effective foragers are good guards as well (Clutton-Brock et al., 1999a). The current hypothesis is that meerkats with a high efficiency at capturing prey are also the best sentinels because they spend less time foraging and thus have more time and energy to spend on other activities (Tatalovic, 2008).

At the same time, sentinel behaviour is not solely altruistic because there are also benefits for the guard itself. Beyond the direct benefit of gaining prestige within the group (Zahavi & Zahavi, 1997), the individual on duty is also the first to recognize potential danger. This gives it the best opportunity to flee first, strongly increasing its chance of survival (Clutton-Brock et al., 1999a).

Many studies deal with the special group structures and group dynamics within meerkat groups and with the exceptional helping behaviour of individuals when raising the offspring. The reproductive suppression of the females in the group by the α-female is also a frequent subject of investigation, as is the exploration of the benefits and costs of cooperation in animals like meerkats.

2.3 Aim of the study

As far as meerkat sentinel behaviour is concerned, only few detailed studies have described the precise behaviour of individuals and groups during guarding sequences. Some information has been published on the alarm calls and the aspect of cooperation in guarding behaviour.

Most of these studies dealt with meerkat groups in the field and sentinel behaviour in the natural environment.

This thesis presents a more detailed investigation of sentinel behaviour in captive meerkat groups. Accurately describing individual and group behaviour during guarding sequences contributes to a better understanding of the need for guard work in captive meerkats. This study is designed to facilitate the comparison of sentinel behaviour between meerkat groups in zoos and groups in the field.

2.4 Meerkats in zoos

Zoos around the world, especially in Europe, are increasingly presenting meerkats as attractions for their visitors because they often have a funny appearance and a kindly and cute face. Moreover, meerkats are diurnal animals with a high activity spectrum and a curious nature. Another aspect for their popularity is their distinctive group life. They are very sociable and communicative within their group and also playful not only as cubs but even as adults. Importantly, meerkats can be presented throughout the year. In winter, they are active too and show themselves if they have enough opportunities to warm up at cold ambient temperatures. Some zoos keep their meerkat groups in socialization with other animals such as different monkey species or other mongoose species that also occur in Africa, attempting to create a more natural environment for all involved species.

2.5 Research hypotheses

To analyse the sentinel behaviour of captive meerkats, I formulated eight hypotheses that encompass different aspects of behavioural patterns. These hypotheses concern individual sentinel behaviour, group sentinel behaviour and the response to bird calls:

- Some individuals are on guard duty more often than others (‘super sentinels’).
- Each guard has its preferred guard spot and guard pose.
- At least one sentinel is always on guard duty.
- Sentinel behaviour is only shown in open-air enclosures.
- The group always stays within a small distance to the current sentinel.
- Meerkats show stronger reactions towards predatory bird calls than songbird calls.
- The group reaction towards bird calls differs in different meerkat groups.
- Some bird species induce stronger reactions caused by bad experiences.

The following investigation covers all hypotheses and is designed to highlight the diverse aspects of sentinel behaviour and its importance for the individual as well as for the whole meerkat group under captive conditions.

3 Material and Methods

The study was conducted in three zoos in Austria and Germany: the Vienna zoo, the Linz zoo and the Augsburg zoo (Figure 2).

Figure 2: The locations of the 3 investigated zoos in Germany (Augsburg zoo) and Austria (Vienna zoo and Linz zoo). Source: Google Earth

The three investigated meerkat groups differ in group composition. While Vienna zoo houses a rather small group, the meerkat groups in Augsburg and Linz are very big compared to many other zoos in Germany and Austria. I chose zoos with similarly structured meerkat enclosures to obtain comparable results. All three enclosures have an inside and outdoor area, which enables observing the interaction between the meerkats and their environment. Each of the three meerkat groups have one α-female, which is the leader of the group. There is only one adult female in each group; all other females are subadult.

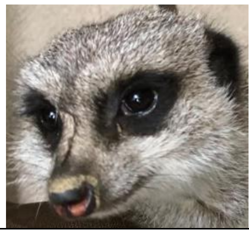
3.1 Study sites

3.1.1 Vienna zoo (Tiergarten Schönbrunn)

a) Study subjects

The meerkat group in Vienna consists of 6 individuals, 2 of which are adults (Table 1). There is one older cub and three younger ones of the same age. The special feature of this group is that the α-female (‘Zuzu’) is not the mother of the cubs.

Table 1: Individual details about the meerkat group at the Vienna zoo.

Number	Name	Sex	Birth date	Birth location	Photo
1	Zuzu	Female (α)	07/09/2015	Leipzig	
2	Chilili	Male	01/06/2013	Vienna	
3	Akio	Male	27/06/2017	Vienna	
4	Binta	Female	16/09/2017	Vienna	
5	Bakadi	Male	16/09/2017	Vienna	
6	Babu	Male	16/09/2017	Vienna	

b) Housing

In the Vienna zoo, both areas (inside and outside) are visible for visitors and surrounded by glass. The enclosure is part of a house with many different monkey species, and the meerkats share their space with a group of King colobus monkeys (*Colobus polykomos*) (Figure 3). The enclosure is divided into three connected areas, the inside area (127 m^2) and two smaller 'outside' areas of different sizes (93 m^2 and 49 m^2).

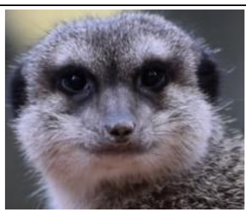
Figure 3: Indoor enclosure of the monkey house at the Vienna zoo. Source: Vienna zoo, photo: Daniel Zupanc

3.1.2 Augsburg zoo

a) Study subjects

The meerkat group in Augsburg consists of 18 individuals (Table 2). With an age of 9 years, the α-female is relatively old but still the undisputed leader of the group.
The other adult animals in the group are males between 2 and 6 years; only some of the young individuals are females.

Table 2: Individual details about the meerkat group at the Augsburg zoo.

Number	Name	Sex	Birth date	Birth location	Photo
1	-	Female (α)	22/07/2009	Erfurt	-
2	-	Male	31/07/2012	Augsburg	
3	-	Male	26/05/2014	Augsburg	

4	-	Male	26/05/2014	Augsburg	
5	-	Male	26/05/2014	Augsburg	
6	-	Male	23/08/2014	Augsburg	
7	-	Male	23/07/2015	Augsburg	
8	-	Male	14/02/2016	Augsburg	
9	-	Male	02/05/2016	Augsburg	
10	-	Female	25/05/2017	Augsburg	-
11	-	Female	25/05/2017	Augsburg	-
12	-	Female	25/05/2017	Augsburg	-
13	-	Female	25/05/2017	Augsburg	-
14	-	Female	20/03/2018	Augsburg	-
15	-	Female	20/03/2018	Augsburg	-
16	-	Male	20/03/2018	Augsburg	-
17	-	Male	26/07/2018	Augsburg	-
18	-	Male	26/07/2018	Augsburg	-

b) Housing

At Augsburg zoo, the inside and outside areas have approximately the same size (inside: 30 m^2, outside: 40 m^2). Both areas are surrounded by a half-height separation made of glass and wood (Figure 4). The meerkats have the opportunity to go outside during the daytime throughout the year. There is no socialization with other animal species.

Figure 4: Meerkat enclosure at the Augsburg zoo. Source: Augsburg zoo

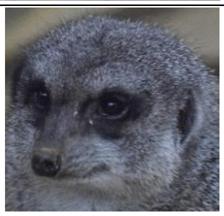
3.1.3 Linz zoo

a) Study subjects

At the beginning of the observation period the group size at Linz zoo consisted of 14 individuals, 7 adults aged between 6 and 9 years with seven cubs (Table 3). The α-female (‘Nadine’) is the only female among the adults; all other adult members are males.

Table 3: Individual details about the meerkat group at the Linz zoo.

Number	Name	Sex	Birth date	Birth location	Photo
1	Nadine	Female (α)	01/01/2013	Linz	
2	Timo	Male	24/06/2010	Linz	

3	Tulan	Male	07/04/2010	Linz	
4	Tilda	Male	07/04/2010	Linz	
5	Turbo	Male	07/04/2010	Linz	
6	Tommy	Male	16/09/2009	Linz	
7	Timon	Male	01/04/2009	Linz	
cubs transferred on December 6th 2018					
8	-	Female	27/04/2018	Linz	-
9	-	Female	27/04/2018	Linz	-
10	-	Female	27/04/2018	Linz	-
11	-	Female	27/04/2018	Linz	-
12	-	Male	01/08/2018	Linz	-
13	-	Male	01/08/2018	Linz	-
14	-	Female	01/08/2018	Linz	-

b) Housing

At Linz zoo, a big outdoor enclosure (121 m^2) is surrounded by a half-height fence made of glass. The inside area is smaller (16 m^2) and located in a small glass house (Figure 5). The meerkats can go outside during the day throughout the year. There is no socialization with other animal species.

Figure 5: Meerkat enclosure at the Linz zoo. Source: Linz zoo

3.2 Data collection

3.2.1 Observation period

Data was collected from October to December 2018 by recording at least 30 video hours per zoo to obtain an appropriate sampling size (Table 4). The small variation in video hours between the three zoos was due to the different weather conditions during the observations.

Table 4: Observation details: the start and end date and the recorded video hours for each zoo.

Zoo	Observation start	Observation end	Video hours
Vienna	19 October 2018	13 November 2018	30:58:56
Augsburg	15 November 2018	26 November 2018	36:14:06
Linz	29 November 2018	11 December 2018	31:32:10

3.2.2 Equipment

For data collection, I used a video camera with two different lenses (Table 5) to ensure high-quality videos at various distances. The camera was fixed to a tripod.

Table 5: Camera type and lenses used during observation.

Type	Nikon D5300
Lens 1	AF-P NIKKOR 18-55mm 1:3.5 - 5.6G
Lens 2	AF-S NIKKOR 55-200mm 1:4 - 5.6GII

For the playback experiments I used a small speaker (Type: Telefunken BS1005M) connected to the smart phone via Bluetooth to play back the audio files.

3.2.3 Individual identification

Males and females are easier to distinguish because of their distinctive characteristics, whereas a discrimination between individuals of the same sex is challenging. Depending on the age and rank within the group, the testicles of the males are visible in some poses (Figure 6). In the described guarding pose (GUA), sexing is easier than in the raised guarding pose (RG).

Figure 6: Individual discrimination of adult meerkats based on sexual characteristics: visible testicles of an adult male.

The main clue to identify individuals was variation in coloration and shape in the eye masks (Figure 7). High-resolution photos were taken to detect the subtle differences in shape and/or coloration. Figure 7 shows four examples of how to differentiate individuals based on their eye masks.

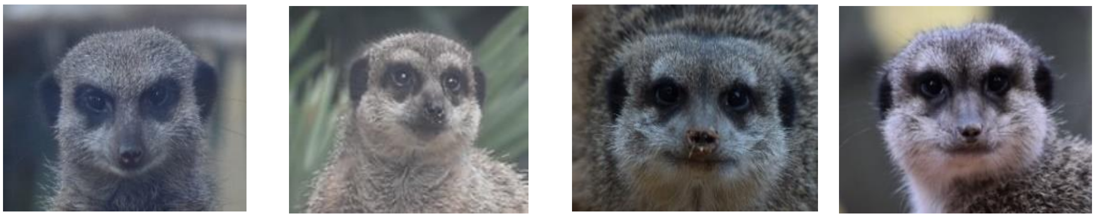


Figure 7: Four examples of meerkat mask types for individual identification.

In addition to the black coloration, some animals show also strongly contrasted stains around the eyes where bright and dark colours come together. In some cases, the coloration of the nose can also help because the black colour of the eye mask can individually reach to the tip of the snout.

Another helpful element for identification was body size. Especially at the Vienna zoo, it was easy to spot the second male and oldest cub 'Akio' because they were the tallest individuals of the group. Whenever the group was close together (e.g. during community guarding), this rapid method of identification was useful.
In individual cases, special morphological abnormalities helped with the identification. In the group at Linz zoo, one individual has lost its left pinna. An individual at Augsburg zoo has a shortened tail.

3.2.4 Ethogram

In order to create an ethogram (Table 6), the meerkat group in Vienna was observed for several hours and all relevant behaviour was recorded. In addition, some general behavioural pattern such as foraging or digging were included in the following ethogram (following Scott, 2014).

Table 6: Ethogram with all relevant behavioural pattern of meerkats concerning sentinel behaviour. Divided into 5 different categories: 'Guard pose', 'Guard number', 'Guard reaction', 'General behaviour' and 'Additional behaviour'.

Guard Pose		
Vigilance (VI)	The animal is sitting on its backside, all four legs are on the ground. It shows repeated head movement or orientation in all directions. The attitude is relaxed but attentive.	
Guarding (GUA)	The individual is sitting on both hind legs. The upper body is upright, the front legs are docked to the body, the tail is for support. The animal shows head movement and changing head orientation (~ every 3 sec).	
Raised guarding (RG)	The animal is standing on hind legs. The body is completely stretched out. The guard often stands on its tiptoes, the tail is for support. It shows rapid head movement and changing head orientation (~ every sec).	
Guard number		
1 Guard (1G)	Only one animal in the group is in guard position. The other group members pursue other activities and give responsibility to a single individual.	

2 Guards (2G)	Two animals of the group take guard position simultaneously and observe the environment independently of each other. The other animals of the group pursue other activities and split up the responsibility for the group to two individuals.	
3 Guards (3G)	Three animals of the group take guard positions and observe the environment independently. The remaining group pursues other activities.	
Community guard (CG)	Several animals (more than 3) of the group up to the entire group take guard position at the same time and observe the environment independently.	
Guard reaction		
Increased attention (IA)	The guard responds to sudden audible or visual signals with reinforced alertness (e.g. aircraft or birds). It shows strong head orientation in the direction of the incoming stimulus. Sometimes also a change of the guard pose (e.g. from sitting to standing) occurs.	
Escape (ESC)	The sentinel leaves the current guarding spot to flee to or in a burrow for hiding as a consequence of a certain external influence.	
Ignore (IGN)	Certain (known) acoustic or visual signals are ignored and disregarded as they are considered non-threatening (e.g. visitors knocking on the windows of the enclosure).	
General behaviour		
Foraging (FO)	Searching for food: scanning and sniffing the ground with frequent stops for digging/scratching in the earth.	
Eating (EA)	Eating prey or fruits. Food object is processed with mouth and/or paws.	
Resting (RE)	Resting phase in a lying position. Either the animal is asleep or in rest position with open eyes.	
Moving (MO)	Movement without interruption. Tail in lowered position.	
Running (RUN)	Fast locomotion. Tail in raised position.	
Grooming (GRO)	Animal cleans itself or another animal of the group with its tongue.	
Scratching (SC)	Weak digging on the surface of the ground with the paws	
Digging (DIG)	Working with the forelegs at a certain place in the ground to dig a hole. The earth is transported away to the back through the hind legs.	
Additional behaviour		
Out of sight (OS)	The animals are not visible in the enclosure or hidden inside their burrows.	

3.3 Methods

3.3.1 General sentinel behaviour

I used focal animal (= the guarding individual) sampling to record the duration of a guard sequence, the guard location, the number of current guards and the associated guard pose. The observation method for data collection in this study involved continuous recording. This recorded all the relevant behavioural patterns (ethogram) of the animals over a certain period, including the frequency and the duration of each behavioural category. Additionally, the group behaviour during the sentinel sessions was also recorded with ad libitum sampling. All the relevant information during observation were entered into a tailor-made observation sheet (Table 7).

Table 7: Observation sheet for all relevant details during the observation period

Date:			**Location:**		**Weather:**	
Video	Time	Enclosure	Guard number	Focus: Guard	Group	Events

Each video was numbered to ensure traceability for the subsequent analysis and included information on the date, location and current weather conditions. A single observation session usually took 20 minutes. In Augsburg zoo and Linz zoo, most of the videos had a duration of 20 minutes, whereas in Vienna zoo more short-term videos were collected. This is because the Vienna meerkat group moved a lot within the different areas of the enclosure. Observing that group required moving with the equipment, causing video interruptions.

For each video the starting time was recorded along with the current location of the meerkat group in the enclosure (inside/outside/inside+outside). The number of current guards was also noted, including the times of guard-change. Based on the special focus on the guard, an extra column was available to enter the actions of the current guard and its associated behaviour changes. The column ‘Group’ encompassed all group behaviours or reactions if something relevant occurred. The focus, however, remained on the guard. The column ‘events’ recorded all external influences from the environment, for example noisy visitors, vehicles, helicopters or other aircrafts. Each event was recorded with its corresponding time of occurrence. If multiple guards were active at different spots in the enclosure, the second guard was observed by taking notes (time, location, pose) but the camera focus remained on the first detected guard. This approach was important for subsequent analysis, e.g. to determine the duration of a guarding period.

3.3.2 Response to playbacks of bird calls

To analyse the behaviour of meerkats towards different bird sounds, I used audio files with sounds of various bird species (Table 8). The birds were divided into two groups:

- songbird species (potentially harmless)
- predatory bird species (potentially dangerous)

The group of songbirds was composed of native Central European species that are common in Austria and Germany. I used sounds of a total of nine different songbirds. The group of predatory birds encompassed a mixture of native Austrian species as well as a few species that also inhabit southern Africa. In total, 15 different calls of predatory birds were applied.

Table 8: Bird species used in the playback experiment separated into the 2 categories songbirds and predatory birds. Source of the audio files: www.vogelstimmen.info

Songbird species	Predator bird species
European Tree Sparrow	White-tailed eagle
European House Sparrow	Steppe eagle
European robin	Golden eagle
Coal tit	Eastern imperial eagle
Eurasian Blue tit	Short-toed snake eagle
Common blackbird	European honey buzzard
Eurasian wren	Long-legged buzzard
Common chiffchaff	Common buzzard
Common chaffinch	Rough-legged buzzard
	Red kite
	Black kite
	Northern goshawk
	Eurasian sparrowhawk
	Common magpie
	Carrion crow

The single bird sound sequences were replayed successively 3 times, each sequence lasting about 10 seconds. The overall duration of one playback sequence was therefore about 30 seconds. Each bird call was played back at least one time in Linz and in Augsburg. A few of the songbird sounds were played back twice because fewer sounds of songbirds than of predatory birds were available.

The speaker was concealed to ensure that the animals were unable to locate the sound source. Importantly, the speaker was not positioned near the observation spot so that the animals could not make a connection between the observer and the replayed sounds. Playback started when there was only a single individual at the guard position.

In order to avoid habituating the meerkat group to the playbacks, I did not run sound experiments on consecutive days. The number of playbacks per day varied between 2-4 bird calls, depending on the reaction towards previous playbacks and high or low visitor frequencies. There was always a break of several minutes between playbacks of different bird sounds. This break enabled the meerkat group to have enough time to relax and engage in normal activity.

The focus of observation was on the current guarding individual, but I tried to record the reaction of the entire group as well. All behavioural changes of the guard and the group were entered on the observation sheet.
I distinguished between the following reactions of the sentinel and the whole group to the playbacks.

For the guard, I defined nine different behavioural categories:

- **No reaction**: sentinel showed no visible reaction to the playbacks.
- **Slow head**: sentinel showed a slow head movement (no visible alertness)
- **Fast head**: sentinel showed a rapid head movement (tension)
- **Body turn**: sentinel turned its body in the raised guarding pose to check all directions
- **Looking up**: sentinel looked up, presumably checking the sky for potential danger
- **Additional guard(s)**: guard number increased by at least one additional individual
- **Guard change**: another individual took over the guard spot, the first one left its position
- **Pose change**: sentinel changed the pose (VI, GUA, RG)
- **Leave/Escape**: sentinel left its guard spot to flee

For the reaction of the group to the playbacks, I defined nine different behavioural categories:

- **No reaction**: whole group showed no visible reaction to the bird sounds
- **Alerted**: some (or all) individuals raised their heads and showed increased vigilance
- **Relaxation time**: time until whole group was back in relax mood after hearing calls
- **Escape to the burrows**: some (or all) animals escaped to the burrows but didn't hide
- **Escape in the burrows**: some (or all) animals escaped and hide in the burrows
- **Look out of the burrows**: the hidden animals stuck their heads out of the holes
- **Freeze**: the animals showed no further movements and remained in place
- **Group back**: time until the whole group was back after hiding in their burrows
- **Out of sight**: no individual of the group was visible

3.4 Data analysis

I used the free software ‘Solomon Coder’ for video coding. All the recorded videos were analysed with the program by structuring them into two parts. The first part comprised the dataset 1 with all videos showing general sentinel behaviour. The second part involved the dataset 2 with all videos that recorded the playback experiments. Two different working sheets were created for the analysis of the general observations and the playback experiments (Figure 8 and Figure 9).

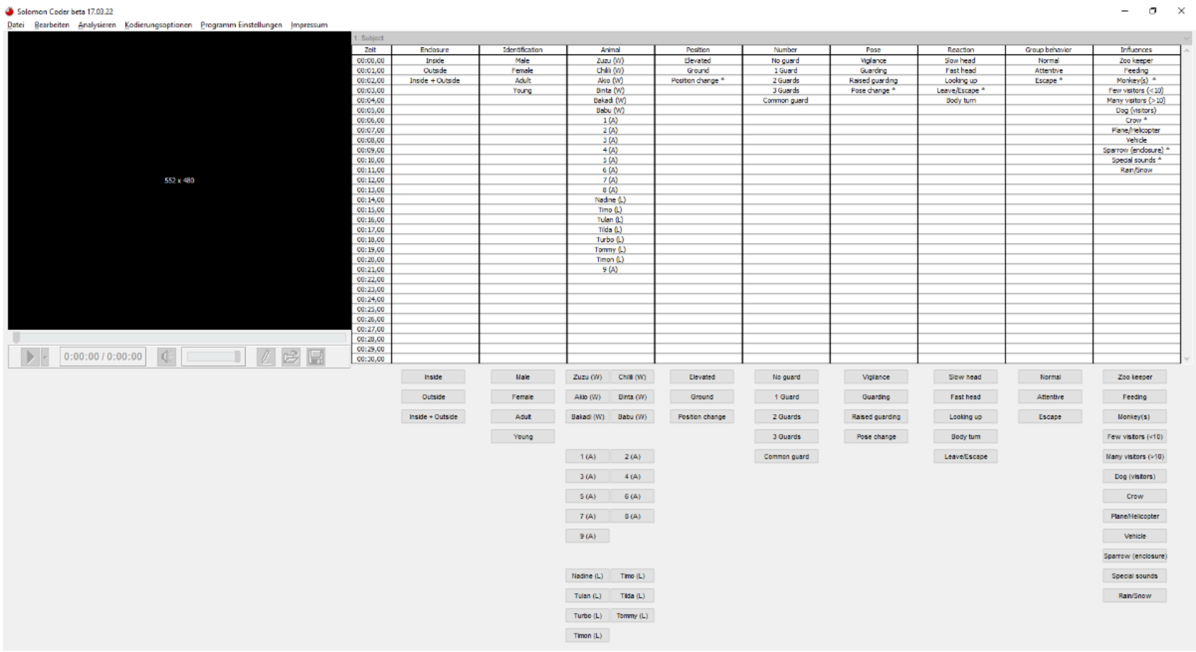


Figure 8: Basic behaviour sheet in ‘Solomon Coder’ with the different categories (Enclosure, Identification, Animal, Position, Number, Pose, Reaction, Group behaviour and external Influences); Left: black window to run the respective video file; Right: work field with duration and the specific behavioural categories; Below: buttons for each category standing for a special event.

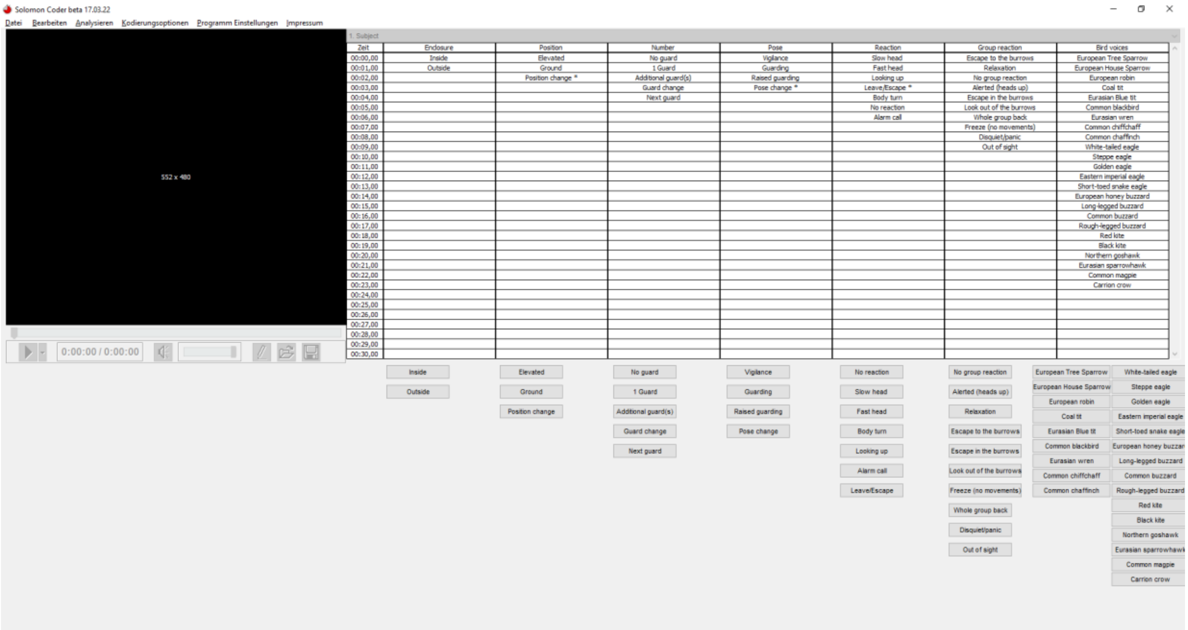


Figure 9: Bird-call-behaviour sheet in 'Solomon Coder' with the different categories for the playback experiment (Enclosure, Position, Number, Pose, Reaction, Group reaction, Bird calls);
Left: black window to run the respective video file; Right: work field with duration and the specific behavioural categories; Below: buttons for each category standing for a special event.

The duration of each behavioural pattern was measured. Within each video sequence the various events were dedicated their behavioural category, respectively. The start and stopping point of each event was directly linked to the running time of the video sequence in order to quantify the duration of every action. Sometimes many events occurred in rapid succession, and in such cases the video was run in slow motion (25% of the original speed) for accurate encoding. The analysis function of the program supplied the durations (in seconds) and percentages of the required information. After encoding all videos, the data were extracted to an excel file and average values, standard errors and percentage distribution of the given data were calculated.

Most of the results of the observed behaviour and other analysed parameters are described in percentage distributions. The percentage values are given in relation to the total observation time and the total guarding time at each zoo, respectively.

Calculating the precise percentages of each behavioural pattern required determining the total guarding time in each meerkat group. The total guarding time indicates the complete duration in which sentinel behaviour was detected (the number of current guards, the position or the pose were not an issue). The sole criterion was the fact that the meerkat group showed sentinel behaviour. The total guarding time is calculated as follows:

$$\text{Total guarding time} = \text{Total observation time} - \text{No guard time}$$

The inside/outside-distribution and the no guard time distribution were divided by total observation time at the respective zoo, other values describing sentinel behaviour like guard position, guard number or guard pose by total guarding time.

The many short-term videos that were recorded at Vienna enabled a more detailed analysis of the sentinel behavioural pattern of every individual. Every short-term video sequence focussed on only one animal, and the analysis software determined different timeframes of action, e.g. the guard pose taken. In contrast, long-term videos recorded guard sequences of several animals. If more than one guard was active during one video sequence, the software was unable to differentiate between the guard poses for every individual. In the other two zoos, it was therefore only possible to analyse the individual time on guard duty (not additional position or pose changes for every animal).

The analysis of the playback experiment examined which behaviour occurred in reaction to which bird call. Accordingly, a 1/0-sampling approach was used in which only the occurrence of a certain behaviour is decisive. Specific reactions or behavioural patterns were tallied with a '+'. The relaxation time and the time until the group was back after hiding was also measured. In the form, the durations were rounded to minutes (the big group sizes in Augsburg and Linz made it difficult to more precisely determine the moment of completely relaxed state of the entire group).

3.5 Statistical analysis

For statistical analysis, Prism 8.0 software (Graph Pad) was used, and the unpaired two-tailed Mann-Whitney t-test (nonparametric) was applied. The P-value for statistical significance was set to $P < 0.05$.

4 Results

The total times and total guarding times are shown in Table 9. These values are the basis for calculating all other data. The total time represents the entire duration of the video material (concerning general sentinel behaviour) at each zoo and represents 100% of the observation time. The longer total observation time in Vienna zoo versus Augsburg zoo and Linz zoo is because the time of the playback videos is not included. The total guarding time is high in all three zoos. The time of no guard was subtracted from the total time to yield the total guarding time.

Table 9: Total time and total guarding time for each zoo. Durations are given in seconds and hours. The percentage values are calculated as a proportion of the total time.

	Vienna zoo			Augsburg zoo			Linz zoo		
Duration	**in s**	**in h**	**in %**	**in s**	**in h**	**in %**	**in s**	**in h**	**in %**
Total time	110535	30.7	100	93079	25.9	100	86008	23.9	100
Total guarding time	93874	26.1	84.9	86319	24.0	92.7	62265	17.3	72.4

4.1 General sentinel behaviour – comparison between the zoos

a. Enclosure area distribution

Figure 10 describes the location of the meerkat groups (i.e. use of the different enclosure areas). The Vienna group spent more time in the open-air area, whereas the Augsburg and Linz groups stayed inside most of the time. In Augsburg and Linz, the groups were sometimes divided: some animals were inside, others preferred to stay outside. In Vienna, the relatively small group stayed together all the time in the same enclosure area.

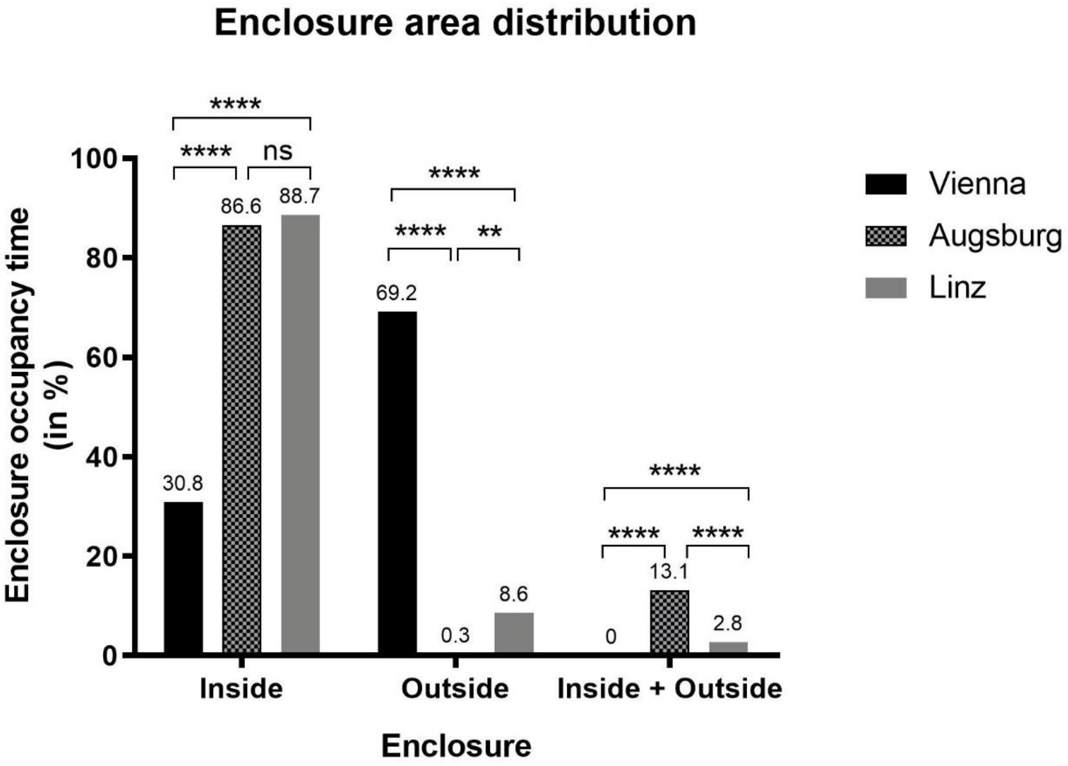


Figure 10: Percentage distribution of enclosure utilization at the three zoos (as a proportion of the total observation time). Bars show where the meerkat groups spent most of their time.
MWU-Test: **** $p \leq 0.0001$ (highest significance); *** $p \leq 0.001$ (high significance); ** $p \leq 0.01$ (significance); ns $p > 0.01$ (no significance).

b. Guard number distribution

The guard number distribution (Figure 11) describes the differences in the number of established guards between the meerkat groups. The pattern in Vienna and Augsburg was very similar (single guards most of the time): two or more simultaneous guards were rarely active there, and community guarding was also rare. Interestingly, the meerkat group in Linz showed a different behaviour. Community guarding was frequent, almost at the same proportion as single guarding. Two or three guards at the same time were less common.

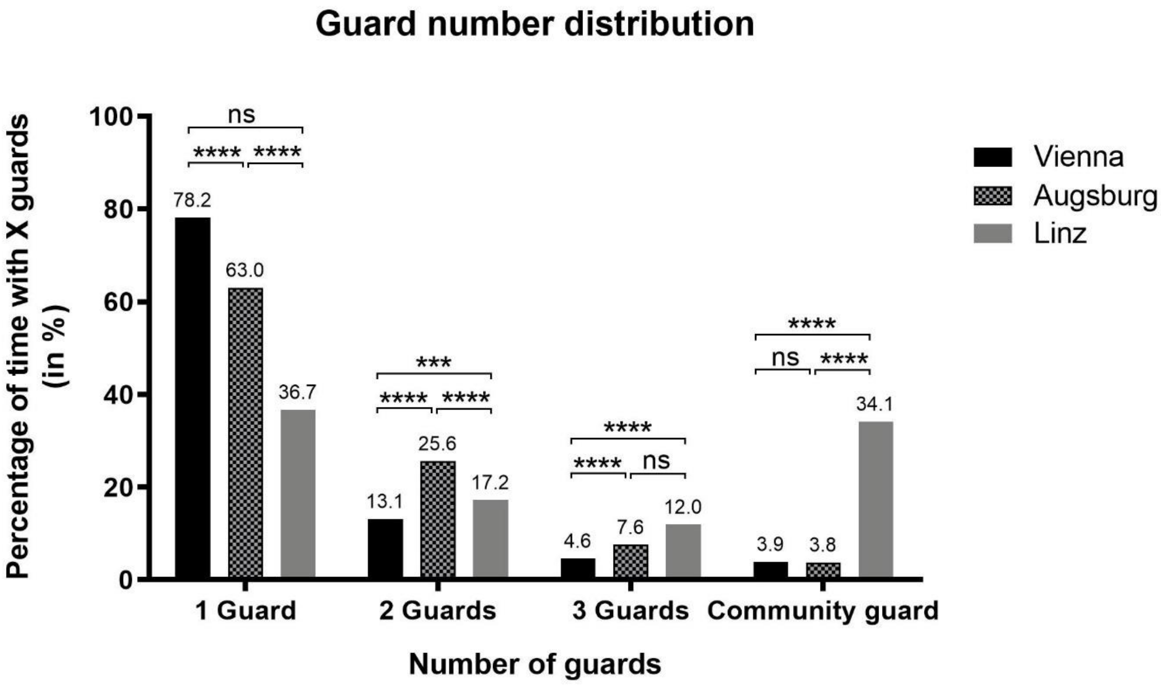


Figure 11: Distribution of the guard number as a proportion of the total guarding time for each zoo. Percentage ratio of each guard number for each zoo in direct comparison.
MWU-Test: **** p ≤ 0.0001 (highest significance); *** p ≤ 0.001 (high significance); ** p ≤ 0.01 (significance); ns p > 0.01 (no significance).

c. Guard position distribution

Figure 12 details the preferred location during guarding sequences. A common feature for all three meerkat groups was that their preferred observation spot was elevated. The high percentage on elevated positions was contrasted by very low ground position values in Vienna and Linz (and zero in Augsburg).

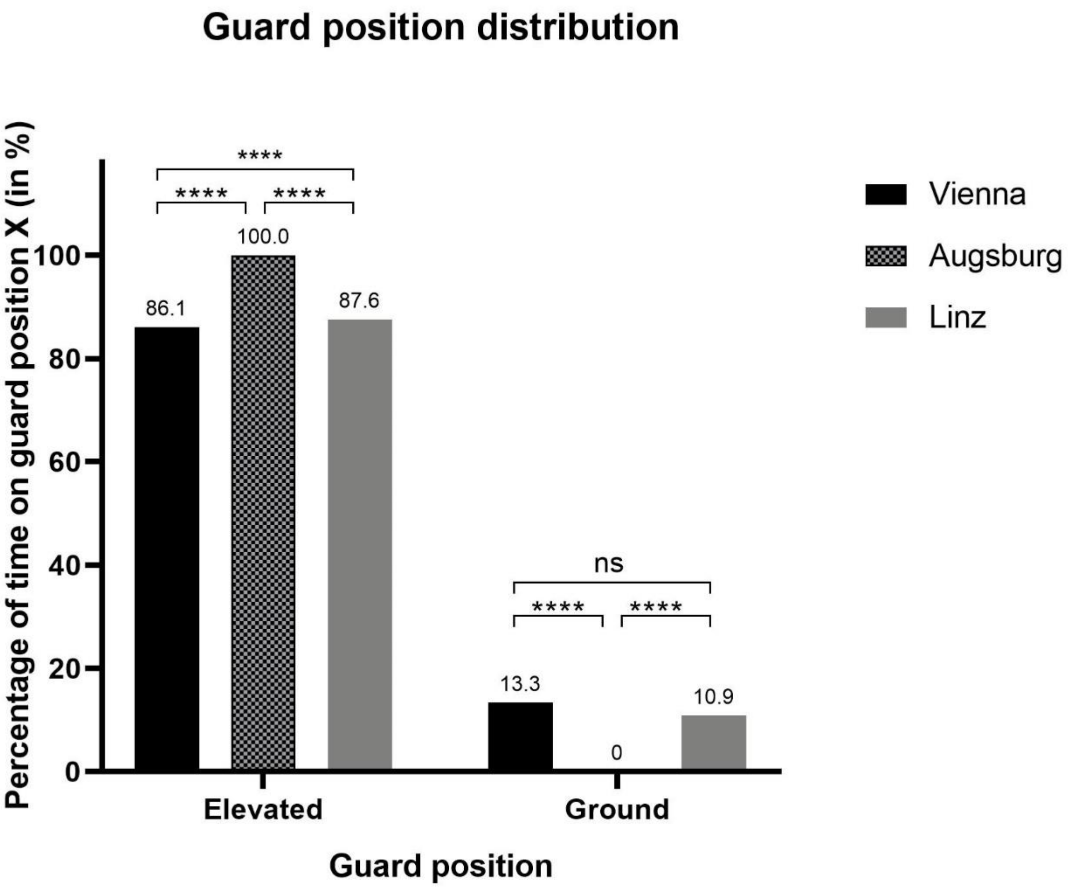


Figure 12: Distribution of the guard positions on elevated spots or on the ground for each meerkat group. The percentage values reflect the proportion of the total guarding time.
MWU-Test: **** $p \leq 0.0001$ (highest significance); *** $p \leq 0.001$ (high significance); ** $p \leq 0.01$ (significance); ns $p > 0.01$ (no significance).

d. Guard pose distribution

The guard pose distribution (Figure 13) describes the different sentinel poses during a guarding sequence. The three groups showed major differences. The Vienna group showed the vigilance pose and the guarding pose in almost the same percentage, whereas the raised guarding behaviour was rare. The Augsburg group exhibited the guarding pose in about one third of their guarding time. The vigilance pose was taken about one quarter of the guarding time, whereas the raised guarding pose was underrepresented. In Linz, yet another pattern emerged. There, the guard mostly took the vigilance pose. The guarding pose made up at least one quarter of the guarding time, while the raised guarding pose was very rare.

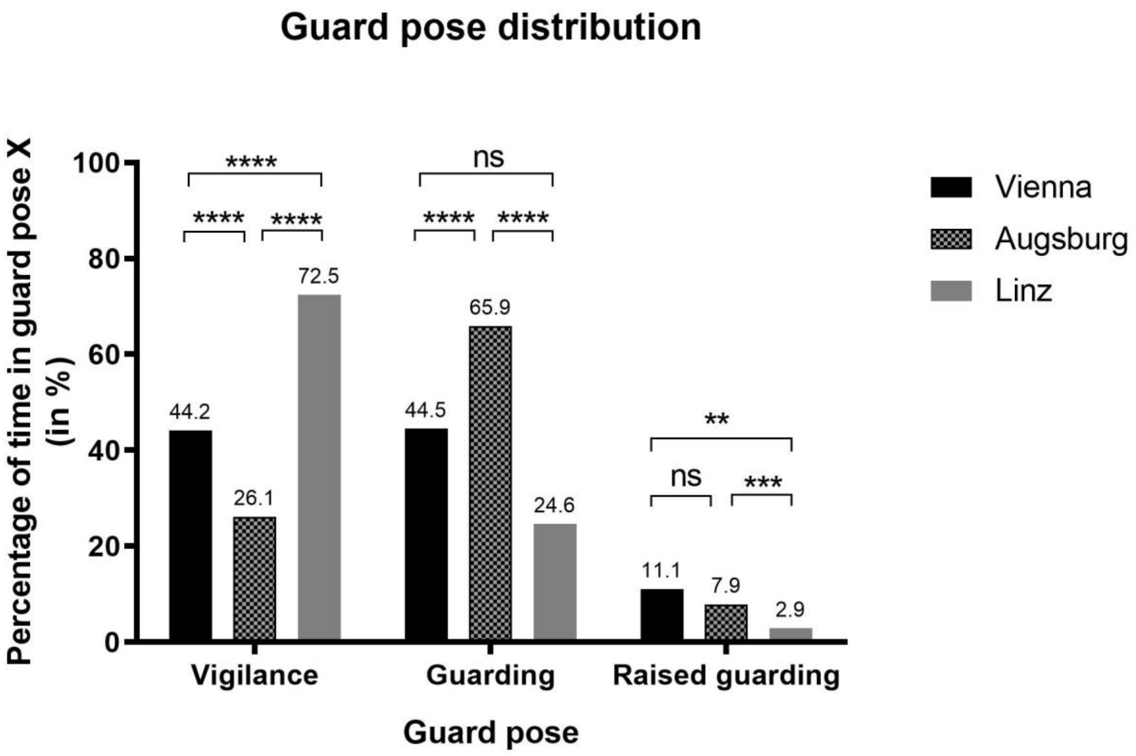


Figure 13: Distribution of the taken guard poses of each meerkat group. Each group of 3 bars represents one pose in the specific zoo to show the percentage in proportion to the total guarding time. MWU-Test: **** $p \leq 0.0001$ (highest significance); *** $p \leq 0.001$ (high significance); ** $p \leq 0.01$ (significance); ns $p > 0.01$ (no significance).

e. Guard time distribution

The distribution of the no guard time (Figure 14) shows a very similar pattern in all three meerkat groups. All usually employed at least one guard with a high percentage. In Vienna, the group employed at least one or more guards most of the time. This was even clearer in Augsburg, where the group very rarely went without a guarding individual. In Linz, the group went without a guard for a longer period of observation time. The percentage without a sentinel was relatively high compared to the other groups and the time with a guard was shorter than at the other zoos.

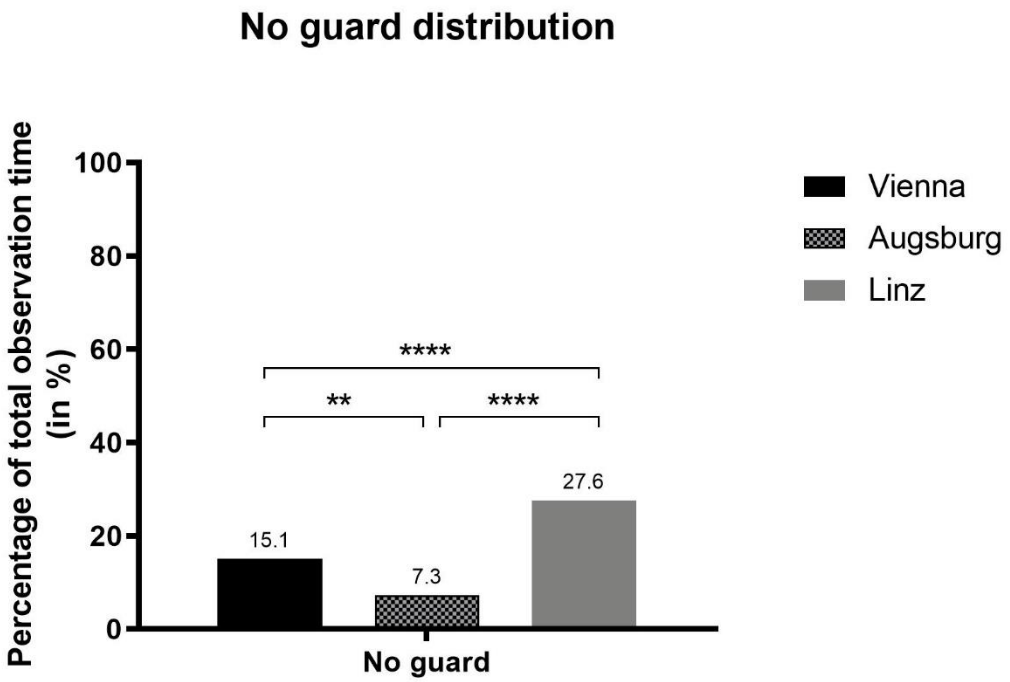


Figure 14: Distribution of the guarding time at the three zoos. The bars show the percentage for 'no guard' in proportion to the total observation time.
MWU-Test: **** p ≤ 0.0001 (highest significance); *** p ≤ 0.001 (high significance); ** p ≤ 0.01 (significance); ns p > 0.01 (no significance).

4.1.1 Single guard sequences

The collected data also provide information about the specific behavioural patterns of every individual in the different meerkat groups. The sentinel behaviour (duration, average guarding time) can be compared for every individual within the group. The Vienna group predominately showed single guard behaviour, making it possible to extract more information about the individuals of the group. The following figures show average durations and percentage values for some of the investigated categories in Vienna, Augsburg and Linz. The calculations are restricted to data showing a single guard.

a. Vienna zoo

Figure 15 shows the average guarding time of the three individuals in the inside and outside area of the enclosure. The average guarding time of 'Zuzu' (α-female), 'Chilili' and 'Akio' differed slightly. The guarding time in the inside area – 2.7 min ± 0.2 (Zuzu), 2.9 min ± 0.6 (Chilili) and 3.2 min ± 0.3 (Akio) – shows approximately the same distribution in all individuals. In contrast, the average guarding time in the outside area was more diverse. 'Akio' guarded about 8.7 min ± 1.1. almost twice as long as the other two individuals (4.0 min ± 0.9 for Zuzu, 4.9 min ± 1.0 for Chilili) in the enclosure's open-air area. Note that the average values of 'Zuzu' and 'Chilili' are similar.

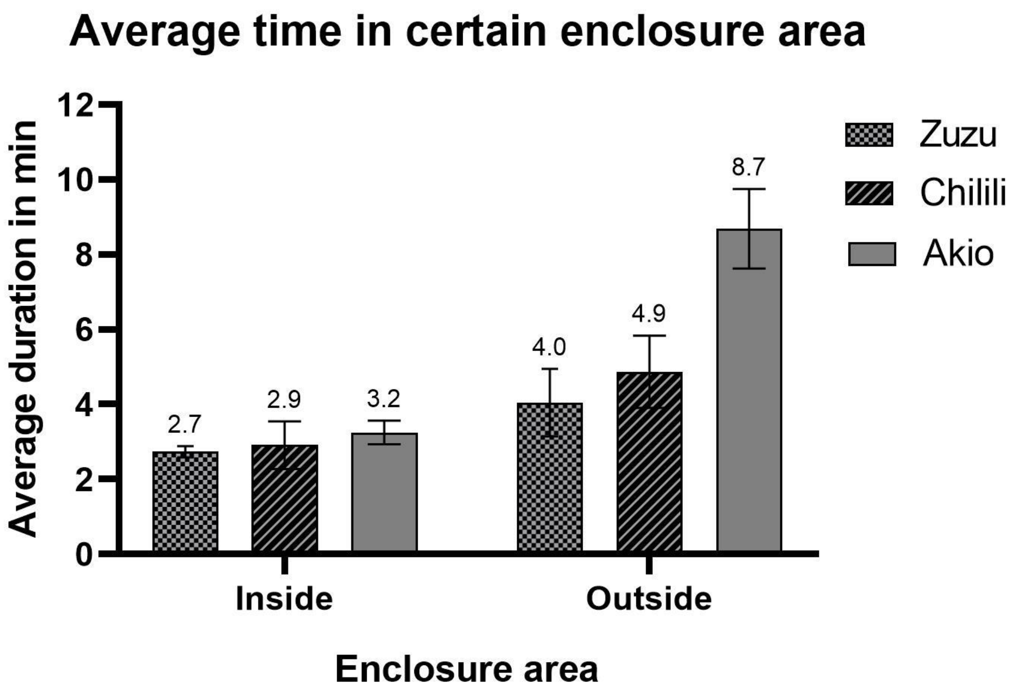


Figure 15: Average guarding duration inside and outside for the individuals ‘Zuzu’, ‘Chilili’ and ‘Akio’ of the Vienna meerkat group. The three individuals (cubs) ‘Binta’, ‘Bakadi’ and ‘Babu’ never showed guard behaviour.

In addition, the average values for the guard position (Figure 16) differed considerably between the individuals. The female ‘Zuzu’ (3.9 min ± 0.9) and the young male ‘Akio’ (7.8 min ± 1.0) spent much more time on guard duty in elevated positions than in ground position. The other male ‘Chilili’ showed no such difference: the average guarding times on elevated and ground position were nearly evenly distributed (3.0 min ± 0.7 and 2.6 min ± 0.5).

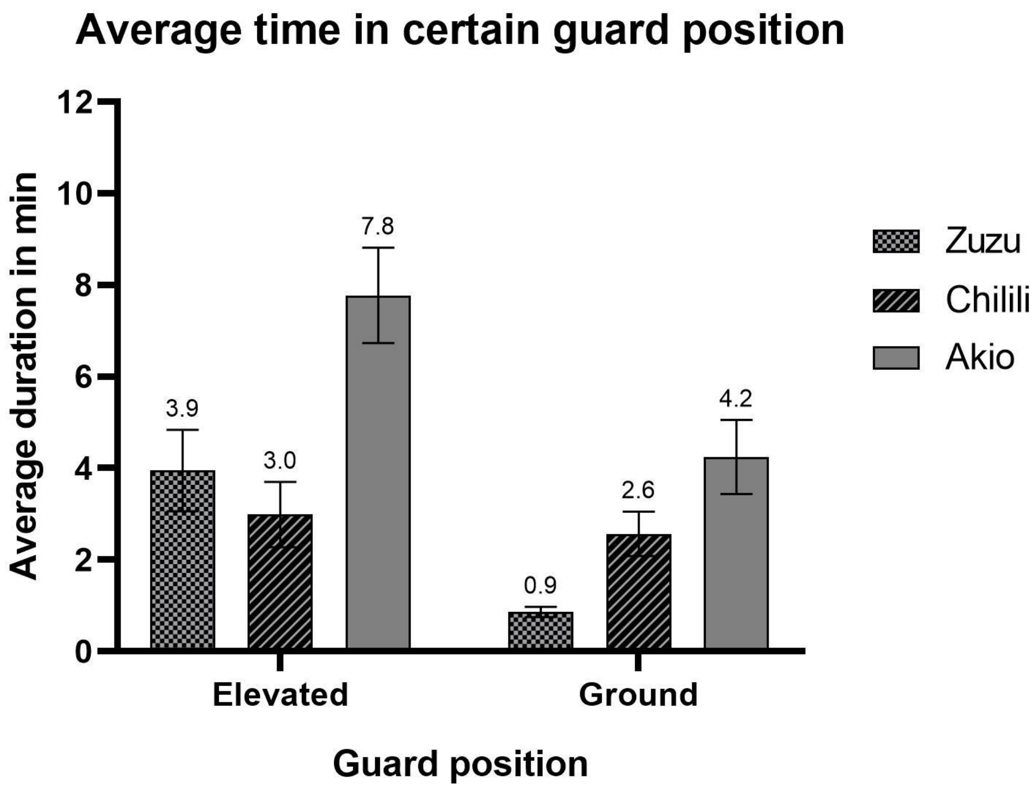


Figure 16: Average guarding duration on elevated or ground position for the individuals 'Zuzu', 'Chilili' and 'Akio' of the Vienna meerkat group.

Figure 17 describes the duration of a certain pose for every individual. The female 'Zuzu' was the only individual using the vigilance pose for long-term guarding. With an average of 3.8 min ± 0.9, she exhibited the vigilance position considerably longer than the two males (0.4 min ± 0.1 and 0.9 min ± 0.3, respectively). However, the two male individuals showed the guarding pose longer: average 3.1 min ± 0.7 ('Chilili') and 5.4 min ± 0.9 ('Akio'). Both males also showed the raised guarding pose – 2.1 min ± 0.5 ('Chilili') and 2.8 min ± 0.5 ('Akio') – whereas the female never guarded in that pose.

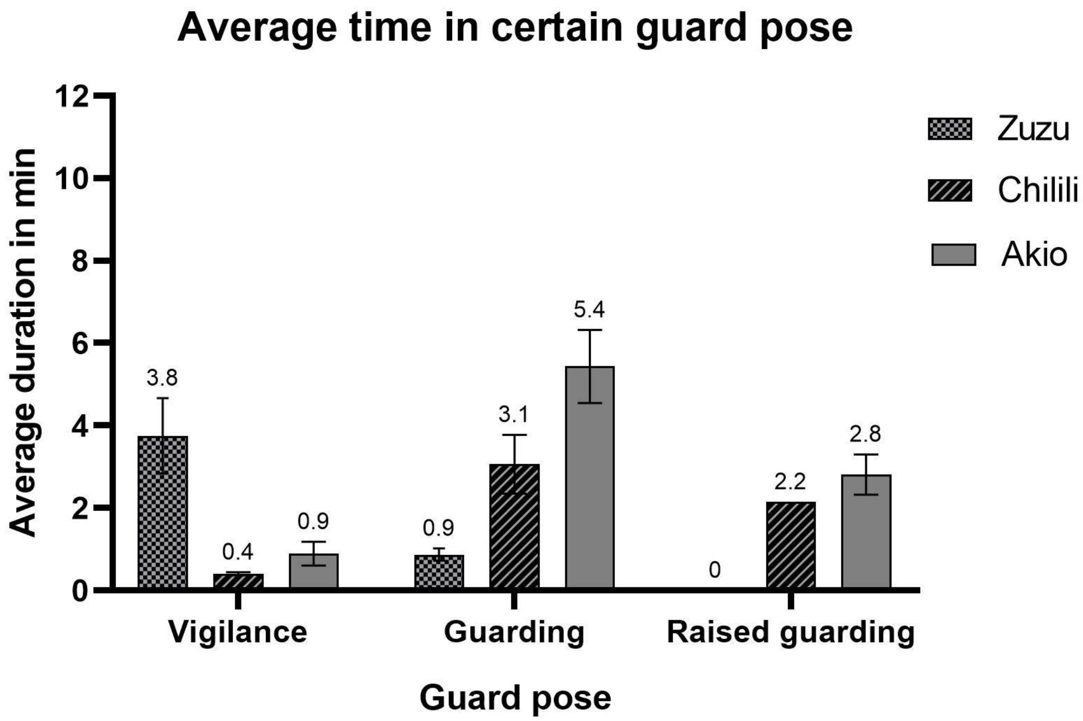


Figure 17: Average guarding duration in the 3 guarding poses Vigilance, Guarding and Raised guarding for the individuals 'Zuzu', 'Chilili' and 'Akio' of the Vienna meerkat group.

The guard position distribution reveals the preferred guarding location during sequences of solitary guards. The guard pose distribution, in turn, shows the preferred guard pose of every individual. Table 10 provides information on single guard sequences. The sex distribution shows that the female kept watch less than the males. The guard position distribution shows that all single guards were mostly in elevated positions. The guard position on the ground was rare.

Concerning the pose during the guard work, the guarding pose was preferred for most of the time in guarding sequences. The vigilance pose and the raised guarding pose were shown less often.

Table 10: Percentage distributions of sex, guard position and guard pose during single guard sequences. All values are given in %.

Sex distribution		Guard position distribution		Guard pose distribution		
Male	Female	Elevated	Ground	Vigilance	Guarding	Raised guarding
79.6	20.1	80.3	19.5	24.0	56.7	19.1

Figure 18 shows which individual spent the most time as a single guard. The young male 'Akio' exhibited the highest proportion of single guarding time. He was established as a solitary guard with a very high percentage, the other two individuals significantly less. The other cubs 'Binta', 'Bakadi' and 'Babu' never served as solitary guards during the observation period.

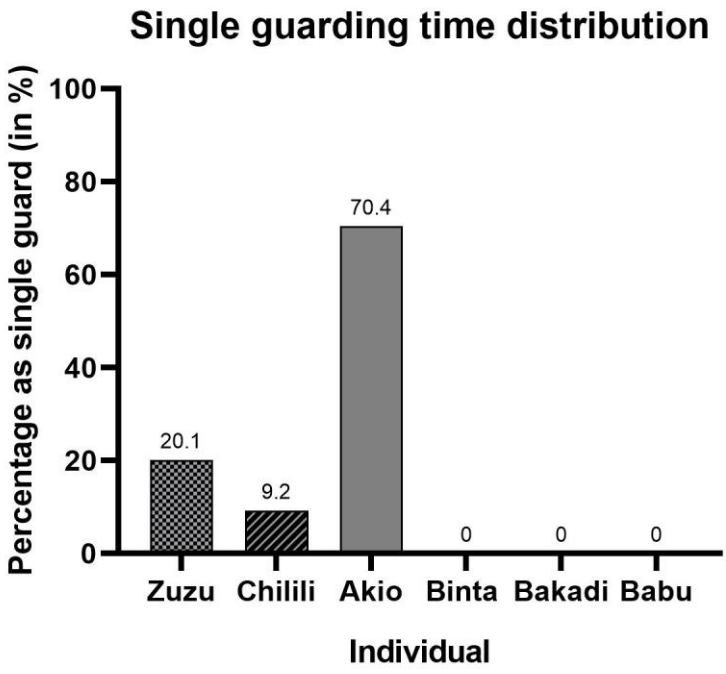


Figure 18: Single guarding duration as a proportion of the total guarding time for each individual of the Vienna meerkat group.

Table 11 details the behavioural pattern of every individual during the single guard sequences. All three animals spent their single guarding sequences mostly in the outside area. The female was very rarely on guard duty in the inside area. The older male had the highest value for inside single guarding, the younger male was in between the female and older male. The distribution of guard positions was similar for all three individuals, while the distribution of the different guard poses revealed differences: in contrast to the two males, the female chose the vigilance pose most of the time.

Table 11: Percentage distributions of enclosure utilization, guard position and guard pose for each individual during single guard sequences. All values are given in %.

Individual	Enclosure distribution		Guard position distribution		Guard pose distribution		
	Inside	Outside	Elevated	Ground	VI	GUA	RG
Zuzu	5.6	94.4	97.9	1.9	93.1	6.8	0
Chilili	15.2	84.8	81.0	18.9	4.0	90.7	5.3
Akio	12.1	87.9	75.1	24.6	6.9	66.5	26.3

b. Augsburg zoo

The meerkat group in Augsburg showed 8 different sentinels during the observation period (Figure 19). The dominant female (individual 1) never worked as a guard, the other adult individuals were on duty for different periods of time. Individual 2 exhibited the highest value: an average of 6.6 min ± 0.7. Individual 6 exhibited the shortest average duration: 2.9 min ± 1.0. The guarding time of the other individuals was in the same range, with average values between 4 and 5 minutes.

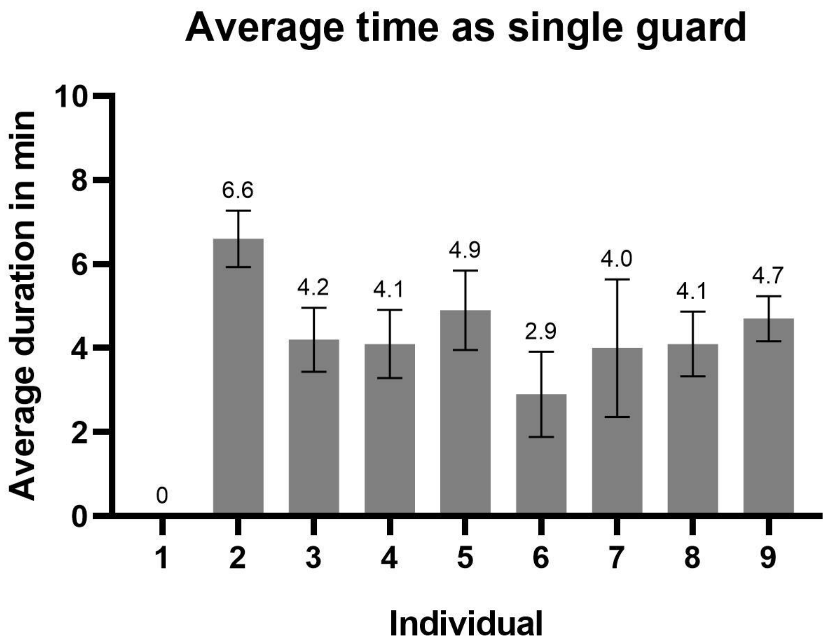


Figure 19: Average duration of single guarding sequences for every individual (1-9) of the Augsburg group. Individual 1 = α-female, individuals 2-9 = adult males.

The percentage distribution of the individuals of the Augsburg group (Figure 20) shows that individual 2 spent the most time single guarding (30.4%). Individual 9 showed an only slightly lower value (28.5%). The rest of the group was rarely on guard duty.

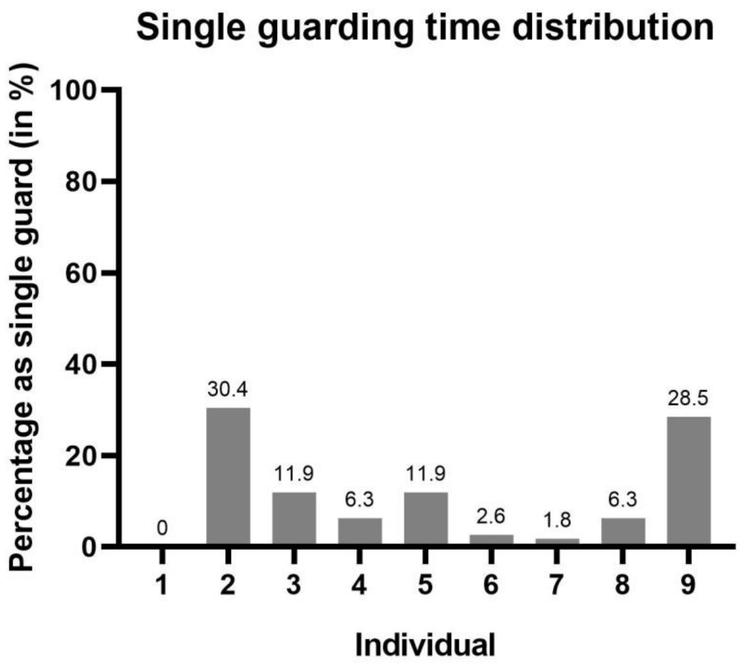


Figure 20: Distribution of single guarding duration in proportion of the total guarding time for every individual (1-9) of the Augsburg group. Individual 1 = α-female, Individuals 2-9 = adult males.

c. Linz zoo

In Linz, 6 adult individuals were identified as sentinels (Figure 21). The dominant female 'Nadine' never showed guarding behaviour. 'Turbo' exhibited the highest average duration of single guarding time: 3.7 min ± 0.4. 'Timon' had the lowest average value (1.1 min ± 0.4). The remaining individuals showed nearly the same average duration values of guarding time, ranging between 2 and 3 minutes.

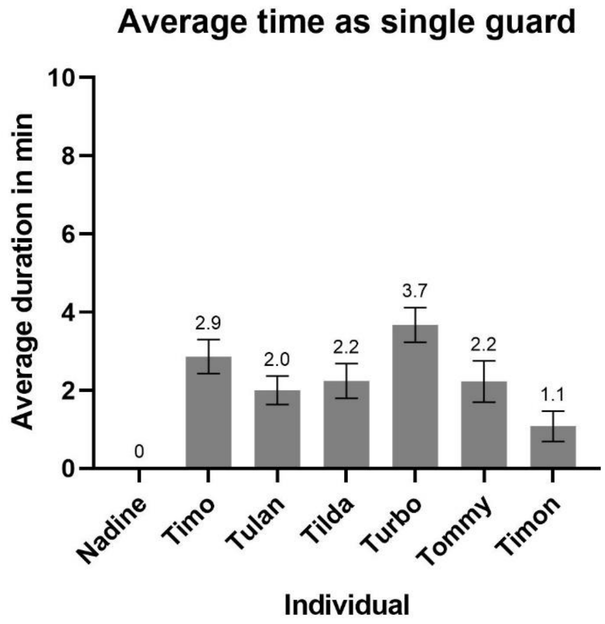


Figure 21: Average duration of single guarding sequences for every individual of the Linz meerkat group. Individual 'Nadine' = α-female.

The percentage distribution of single guarding time at Linz (Figure 22) showed that mainly the individuals 'Timo' and 'Turbo' were on guard duty. All other individuals worked considerably less as sentinels.

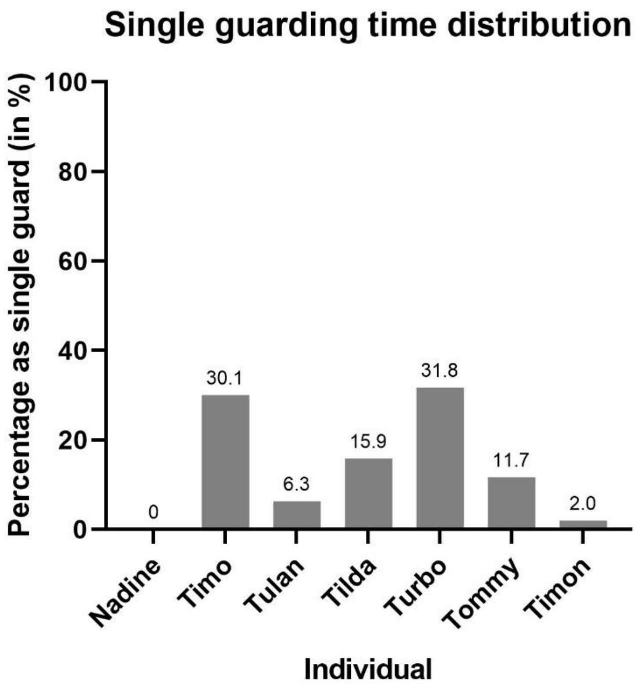


Figure 22: Distribution of the single guarding duration as a proportion of the total guarding time for every individual of the Linz group. Individual 'Nadine' = α- female.

4.2 Behavioural response to playbacks of bird calls

4.2.1 Sentinel reaction to bird calls

Table 12 represents the results of the Augsburg meerkat group. Five songbird species (European tree sparrow, Common blackbird, Eurasian wren, Common chiffchaff, Common chaffinch) did not induce a behavioural response of the guard. All other playbacks led to a certain guard reaction.

These reactions involved ‘slow head movement’, ‘fast head movement’, ‘body turning’, ‘looking up’ and ‘guard change’. ‘Additional guard(s)’, ‘pose changes’ and ‘escape’ from the guarding spot were never observed as a reaction to songbird calls. All predatory bird calls induced a specific reaction of the guard. Especially frequent were ‘fast head movements’, ‘looking up’ and ‘additional guard(s)’. A ‘pose change’ was occasionally observed, and in the case of a Golden eagle call, the guard fled. Taken together, the Augsburg meerkat group showed considerably different reactions to calls of predatory birds versus songbirds.

Table 12: Results of the playback experiment in Augsburg with the sentinel reaction towards the different bird sounds. The bird species (songbirds and predatory birds) are given along with the sentinel reactions. The call of the Rough-legged buzzard was not played in Augsburg.

Augsburg zoo		Guard reaction								
Bird species		No reaction	Slow head	Fast head	Body turn	Looking up	Additional guard(s)	Guard change	Pose change	Leave/ Escape
songbirds	European tree sparrow	+								
	European house sparrow		+			+		+		
	European robin		+			+				
	Coal tit			+	+					
	Eurasian blue tit			+						
	Common blackbird	+	+			+				
	Eurasian wren	+	+							
	Common chiffchaff	+	+							
	Common chaffinch	+	+							
predatory birds	White-tailed eagle			+		+	+		+	
	Steppe eagle			+		+	+		+	
	Golden eagle			+	+				+	+
	Eastern imperial eagle			+	+	+	+		+	
	Short-toed snake eagle		+				+			
	European honey buzzard			+		+				
	Long-legged buzzard			+			+			
	Common buzzard			+		+	+			
	Rough-legged buzzard	-	-	-	-	-	-	-	-	-
	Red kite			+		+				
	Black kite		+			+				
	Northern goshawk			+			+			
	Eurasian sparrowhawk			+		+				
	Common magpie			+		+	+		+	
	Carrion crow			+	+	+	+			

Table 13 describes the guard behaviour at Linz. Only the calls of the European house sparrow induced no reaction of the guard: all other bird sounds caused distinct reactions. The most frequent reaction was the ‘escape’ of the guard. In 15 out of 21 cases (71,4%), the guard left its spot to escape. Interestingly, the guard also left in response to songbird calls. Other reactions were ‘fast head movement’, ‘body turning’, ‘looking up’, ‘additional guard(s)’, ‘guard change’ and ‘pose changes’.

Table 13: Results of the playback experiment in Linz showing the sentinel reaction towards the played-back bird sounds. Calls of Common chaffinch, Black kite and Common magpie were not played in Linz.

Linz zoo		Guard reaction								
	Bird species	No reaction	Slow head	Fast head	Body turn	Looking up	Additional guard(s)	Guard change	Pose change	Leave/ Escape
songbirds	European tree sparrow									+
	European house sparrow	+								
	European robin									+
	Coal tit			+		+				
	Eurasian blue tit									+
	Common blackbird									+
	Eurasian wren									+
	Common chiffchaff			+		+	+		+	
	Common chaffinch	-	-	-	-	-	-	-	-	-
predatory birds	White-tailed eagle									
	Steppe eagle			+			+	+	+	
	Golden eagle			+	+	+			+	+
	Eastern imperial eagle									+
	Short-toed snake eagle									+
	European honey buzzard									+
	Long-legged buzzard									+
	Common buzzard									+
	Rough-legged buzzard			+		+	+		+	
	Red kite									+
	Black kite	-	-	-	-	-	-	-	-	-
	Northern goshawk									+
	Eurasian sparrowhawk									+
	Common magpie	-	-	-	-	-	-	-	-	-
	Carrion crow			+		+				+

4.2.2 Group reaction to bird calls

Table 14 and Table 15 present the reaction of the groups to the specific bird sounds. Table 14 summarizes the Augsburg results: 8 out of 9 songbird species induced no group reaction (exception Eurasian blue tit). In contrast, all predatory bird species induced a group reaction, the most frequent being ‘higher alertness’ with elevated heads. The time that passed until the group was back in relaxed state (relaxation time) was very short, typically about one minute. Only after playing the calls of the Golden eagle was the relaxation time somewhat longer. The two species that induced an ‘escape to the burrows’ were the Golden eagle and Northern goshawk. Another frequent reaction was ‘freezing behaviour’. No extreme reactions such as ‘escape’ and ‘hiding in their burrows’ was observed.

Table 14: Results of the playback experiment in Augsburg showing the reactions of the whole meerkat group to played-back bird sounds. The call of the Rough-legged buzzard was not played in Augsburg. 'Relaxation time' and 'time of return' are rounded in minutes.

Augsburg zoo		**Group reaction**								
	Bird species	No reaction	Alerted	Relaxation time (in min)	Escape to the burrows	Escape in the burrows	Look out of the burrows	Freeze	Return time (in min)	Out of sight
songbirds	European tree sparrow	+								
	European house sparrow	+								
	European robin	+								
	Coal tit	+								
	Eurasian blue tit		+					+		
	Common blackbird	+								
	Eurasian wren	+								
	Common chiffchaff	+								
	Common chaffinch	+								
predatory birds	White-tailed eagle		+	1				+		
	Steppe eagle		+	2						
	Golden eagle		+	3	+			+		
	Eastern imperial eagle		+	2				+		
	Short-toed snake eagle		+	1						
	European honey buzzard		+	1						
	Long-legged buzzard		+	1						
	Common buzzard		+	1						
	Rough-legged buzzard	-	-	-	-	-	-	-	-	-
	Red kite		+	1				+		
	Black kite		+	1						
	Northern goshawk		+	1	+			+		
	Eurasian sparrowhawk		+	1						
	Common magpie		+	2				+		
	Carrion crow		+	1				+		

Table 15 presents the reactions towards playback bird calls in Linz. Only the European house sparrow induced no reaction, whereas the other bird species stimulated different reactions, the most frequent being 'increased alertness'. This reaction was shown towards both songbird and predatory bird calls. The 'relaxation time' ranged from 1-4 minutes. The species whose call implicated the longest relaxation time was the Golden eagle with 4 minutes. The Eastern imperial eagle, the Short-toed snake eagle and the Long-legged buzzard also caused a more severe reaction characterized by 3 minutes of recovery. Other more frequent reactions were 'escape towards the burrows', 'escape into the burrows', 'looking out of the burrows' and 'freezing behaviour'.

Overall, the meerkat group in Linz showed stronger reactions than that in Augsburg. The strongest reaction was to Common buzzard calls: the group fled into its burrows and were out of sight, reappearing only after 40 minutes. The second strongest reaction was in response to carrion crow calls: they returned only after 14 minutes of hiding. The response to calls of the Golden Eagle, Red kite or Northern goshawk was also flight, but the group already reappeared after a few minutes.

Table 15: Results of the playback experiment in Linz showing the reactions of the whole meerkat group to played-back bird sounds. Calls of Common chaffinch, Black kite and Common magpie were not played in Linz. 'Relaxation time' and 'time of return' are rounded in minutes.

Linz zoo		Group reaction								
	Bird species	No reaction	Alerted	Relaxation time (in min)	Escape to the burrows	Escape in the burrows	Look out of the burrows	Freeze	Return time (in min)	Out of sight
songbirds	European tree sparrow		+			+	+		1	+
	European house sparrow	+								
	European robin		+	1						
	Coal tit		+	1						
	Eurasian blue tit			3	+					
	Common blackbird					+			1	
	Eurasian wren		+	1	+					
	Common chiffchaff		+	2				+		
	Common chaffinch	-	-	-	-	-	-	-	-	-
predatory birds	White-tailed eagle									
	Steppe eagle		+	2				+		
	Golden eagle		+	4		+	+	+	3	+
	Eastern imperial eagle		+	3	+			+		
	Short-toed snake eagle		+	3	+			+		
	European honey buzzard			1	+					
	Long-legged buzzard		+	3	+			+		
	Common buzzard					+	+		41	+
	Rough-legged buzzard		+	1						
	Red kite					+			1	
	Black kite	-	-	-	-	-	-	-	-	-
	Northern goshawk					+	+		2	
	Eurasian sparrowhawk		+	1	+			+		
	Common magpie	-	-	-	-	-	-	-	-	-
	Carrion crow					+	+		14	

In Augsburg and Linz, many of the bird calls induced strong group reactions. Figure 23 shows the time to relaxation for each bird call at Augsburg and Linz. It shows that the two meerkat groups differed somewhat in their 'relaxation time'. While the songbird calls caused no reaction at Augsburg, the group reacted quite strongly in Linz. More specifically: in five experimental trials, the relaxation time exceeding 3 minutes. The calls of the Eurasian blue tit, Golden eagle, Eastern imperial eagle, Short-toed snake eagle and Long-legged buzzard induced the strongest reactions, with relaxation times of 3-4 minutes. Only once did the Augsburg group show a strong reaction comparable with that in Linz: the Golden eagle triggered a relaxation time of 3 minutes.

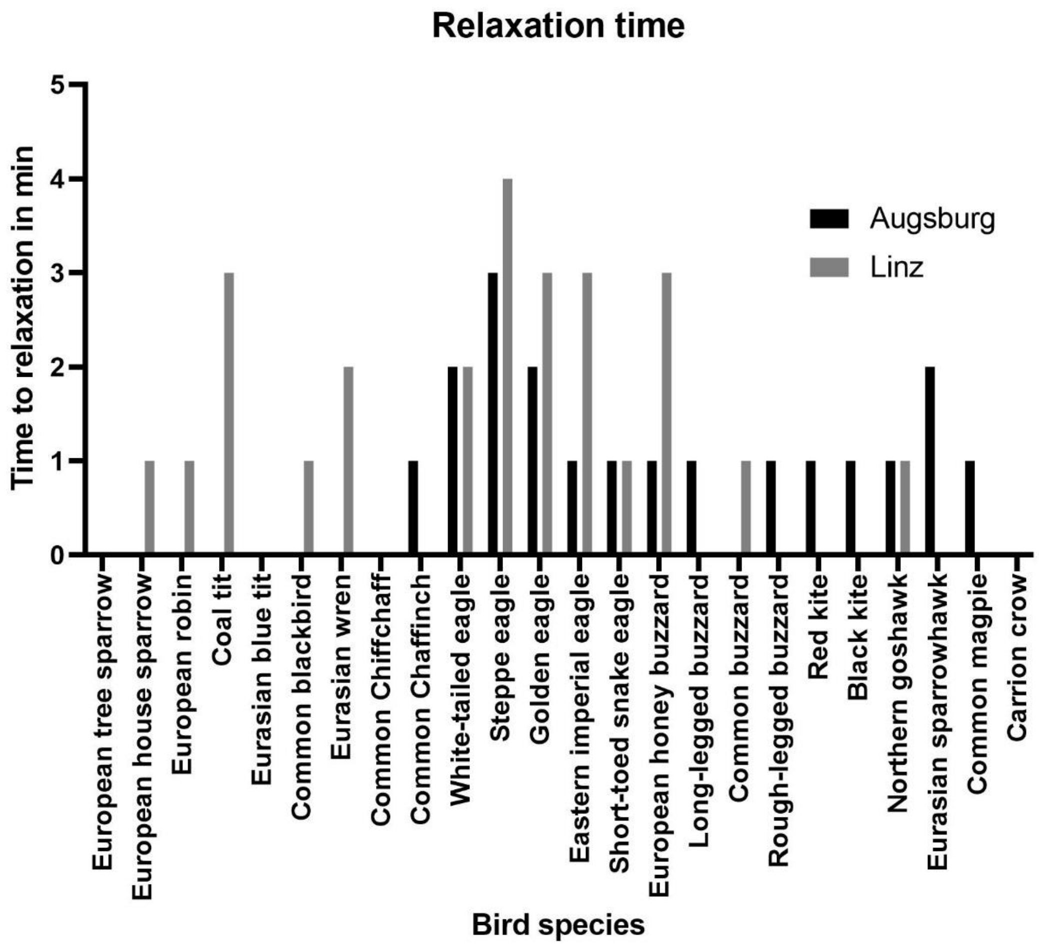


Figure 23: Time that passed until the whole meerkat group was back in a relaxed state after playing-back bird calls. Black bars: Augsburg group, grey bars: Linz group. Rounded in minutes.

At Linz zoo, the group showed additional very strong reactions to the bird call playbacks than the group in Augsburg, e.g. ‘escape’ towards or into the burrows. This enabled calculating the time until the whole group re-emerged from their holes after escaping. Figure 24 shows the duration of the returning time after hearing certain bird calls. The Common buzzard clearly induced the strongest reaction of all bird sounds in Linz. The whole group fled and hid in its burrows for 41 min. All other reactions were less severe. The second highest return duration was induced by Carrion crow calls: the group disappeared for 14 minutes. The reactions to the other species such as the European tree sparrow, Common blackbird, Golden eagle, Red kite and Northern goshawk were weaker, with the group re-appearing after a few minutes.

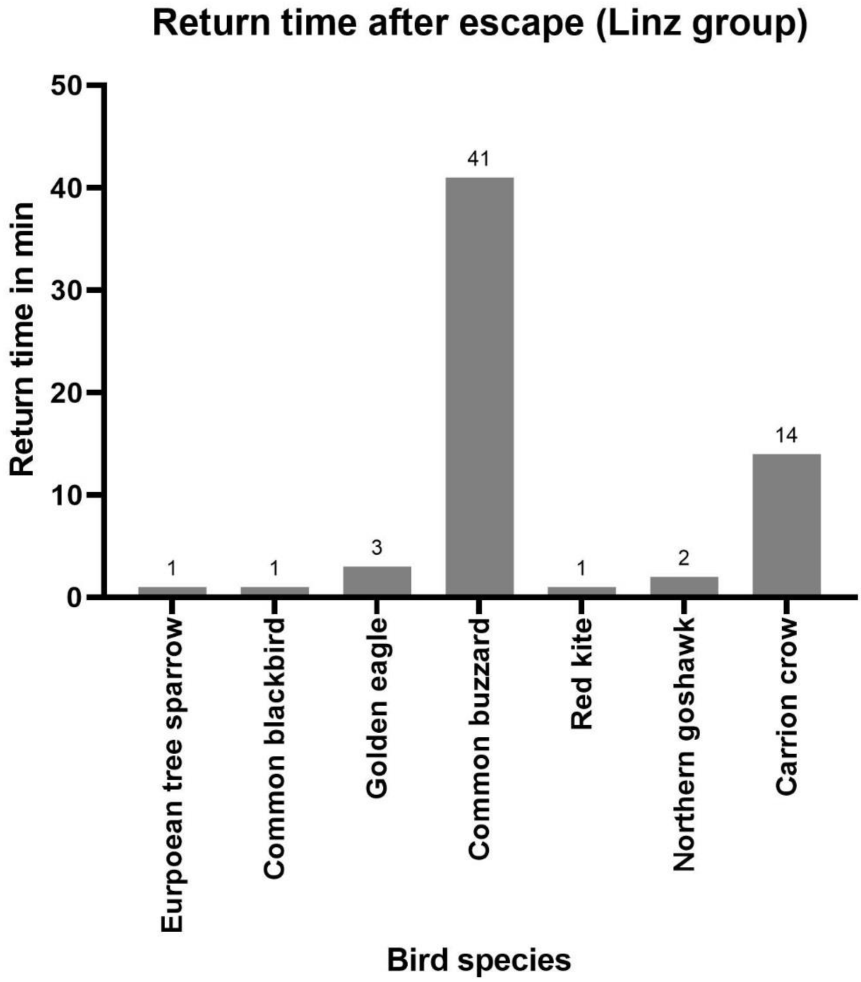


Figure 24: Time until the whole group in Linz re-emerged from its burrows after escape from the played-back bird calls. Rounded in minutes.

5 Discussion

5.1 Individual sentinel behaviour

5.1.1 'Super sentinels'

One of the most striking observations was that some individuals were on guard duty more often than others. The occurrence of so-called 'super sentinels' in meerkat groups (Tatalovic, 2008) and the fact that some individuals do guard work more often was already reported for free-ranging meerkat groups (Clutton-Brock et al., 1999a). The present study definitively supports this observation and shows that 'super sentinels' also exist in captivity. Specific individuals of each observed captive group showed higher percentages of guarding time compared to the remaining group members, with males preforming as sentinels more often. Only at Vienna zoo did a female work as sentinel as well (Table 2), whereas in Augsburg and Linz the guards were always males. This indicates that guarding might be predominately a male behaviour and that females do sentinel work only if their help is needed (for example in small groups as was the case at Vienna zoo). Observations of sentinel behaviour in wild meerkats confirm the present results. They showed that subordinate older males were on guard duty the most, dominant males rarely (Dennis & MacDonald, 1999). Adult females act as sentinels in the wild but usually spend less time guarding than males. The rarest guards were young animals of both sexes, indicating that maturity plays a role in this task (Dennis & MacDonald, 1999).

In all three zoos, specific individuals were on guard duty significantly more often and for longer time periods than others. Thus, my hypothesis that there are 'super sentinels' in each captive meerkat group could be confirmed. These certain meerkats therefore assume more responsibility (Table 2, Figure 11, Figure 13). This observation supports the earlier assumption that these 'super sentinels' spend less time with foraging because they are more effective and therefore have more time for guard work (Clutton-Brock et al., 1999a). Another reason for the higher proportion of sentinel work could be the higher attentiveness of some animals. This may depend on the different individual levels of stress hormones, which are thought to explain different levels of vigilance (Tatalovic, 2008). A recent study showed that stress hormones such as cortisol affect the cooperative behaviour in subordinate meerkats (Dantzer et al., 2017). Thus, sentinel behaviour might be influenced by stress hormone concentrations as well. Investigating stress hormones could provide more information on the vigilance and alertness of individual meerkats.

Other studies showed that sentinels in wild groups suffer higher rates of predation than other group members (Ferguson, 1987). This makes being a sentinel risky, and the more often an individual is on duty, the higher the predation risk. In meerkats, however, the 'super sentinels' accept this increased risk, explaining why many studies have dealt with the question whether meerkat sentinel behaviour is a special form of altruism or whether selfish aspects have priority (Clutton-Brock et al., 1999a). Various evolutionary models such as natural selection or group selection (Wilson & Sober, 1998), theory of kin selection (Hamilton, 1964) or the theory of reciprocal altruism (Zahavi & Zahavi, 1997) have attempted to explain this (presumable) altruistic behaviour and the complexity of group life in meerkats. There are clearly benefits for the sentinel as well. Bednekoff (1997) even suggested that sentinels have lower predation risks because of their experience and the advantage inherent in being the first to detect potential danger. Furthermore, sentinels are captured by terrestrial predators less often than other members of the group due to their elevated position and often closer distance to the burrow (Clutton-Brock et al., 1999a).

In captive meerkats, predation risk plays a lesser role because the group is safe most of the time. Nevertheless, the investigated groups established guards and the results revealed 'super sentinels' in captive groups as well. What drives this 'hero behaviour' in the safety of captivity? One potential explanation is that certain individuals seek to gain reputation within the group by working as reliable guards. The sentinel can benefit by demonstrating its quality as a mating partner, group member or rival (Zahavi & Zahavi, 1997). Thus, the work as 'super sentinel' might influence hierarchy, providing a hypothesis why meerkat 'super sentinels' exist not only in the wild but also in captive communities.

5.1.2 Individual differences

The guard work *per se* is potentially an imprinted feature in meerkats, but whether there are individual differences in performing this job is still being debated.

The present study showed that guard work was generally performed on elevated positions in all three investigated meerkat groups; guard work on the ground was rarely observed only at the Vienna and Linz zoos (Figure 3), underlining that captive sentinels prefer higher spots. The more detailed analysis of the Vienna group showed that most of this work was done on elevated positions, and the tendency to preferred upper locations stood out (Figure 7) (Table 3). Earlier studies in free-ranged meerkats concluded that sex also influences guard positions: subordinate older males always visited the highest points for their sentinel work, while adult females tended to use lower spots (Dennis & MacDonald, 1999). My observations on captive meerkats were unable to fully confirm that theory because, during the observation period, the female often used the top of the biggest rock as a preferred look-out, whereas the subordinate male often used a certain heap of earth on the ground in the outside area of the enclosure.

Meerkats use tree branches, fallen tree trunks, rocks or the top of termite constructions (in their natural habitats) as elevated look-outs (Dennis & MacDonald, 1999). The present observations showed that it is important for zoos to provide various furnishings in meerkat enclosures to enable the animals to behave naturally by taking elevated guard positions. From elevated positions, meerkats are able to scan the horizon. Their great depth perception enables them to detect predators early and from afar (Meder, 1993).

Concerning the chosen guard pose, the results showed differences between the three investigated meerkat groups. Every group showed a different pattern involving the three described poses ‘Vigilance’, ‘Guarding’ and ‘Raised guarding’ (Figure 4). Within the Vienna group, individual preferences were recognizable (Figure 8): the female used the vigilance pose most of the time, whereas the two males most often assumed the guarding pose (Table 3). One consideration is that the level of alertness during guard work could be decisive for the pose. Individuals with experience tend to take a more relaxed pose (such as the vigilance pose) faster than inexperienced ones (younger group members). This may help explain why younger group members rarely serve as sentinels (Dennis & MacDonald, 1999). They might be less reliable due to missing experience. The vigilance pose seems to be the most relaxed guard pose, while the raised guard pose seems to represent extreme alertness and tension. The most observed pose is ‘Guarding’, which is intermediate between the other poses. Therefore, the postulated hypothesis that each guard has individual preferences concerning location and taken pose during guard work could be confirmed.

5.2 Group sentinel behaviour

Meerkats must be highly attentive to avoid becoming victims of various predators in their natural habitat. Potential danger can occur at any time from every direction: predatory birds from above or wild dogs, jackals and snakes from the ground (Wilson & Mittermeier, 2009). Group survival therefore depends on installing sentinels. One might assume that more guards mean better protection, but that does not apply automatically to meerkats. The present results showed that most of the time only one sentinel was present (Figure 2). In both Vienna and Augsburg, the period with a single guard was high, underlining that the groups preferred this arrangement. The Linz group, by contrast, showed equal time periods of single and community guarding. These findings suggest that different meerkat groups have distinct preferences regarding sentinel behaviour. One potential explanation is that the group size is decisive. It may well be that small groups tend to employ only solitary guards whereas bigger groups can afford more sentinels. Small groups naturally have fewer possibilities of exchanging the sentinel, leading to more guard work with longer and more frequent periods for every individual per day. It therefore makes sense for meerkats in the wild to have bigger group sizes with up to 30 individuals, with natural selection favouring larger over smaller groups (Estes, 2012). The latter show higher mortality rates and an increased threat of group extinction through droughts or predators (Clutton-Brock et al., 1999b). The observations on the small Vienna group confirmed that behavioural pattern for captive meerkats as well. Interestingly, the preference of the bigger Augsburg group to also set up one sentinel most of the time contradicts the assumption that bigger groups tend to establish more than one guard.

The present investigation also revealed that the meerkat groups had at least one guard on duty most of the time and that periods without any guard were very short (Figure 5). Thus, the hypothesis that captive meerkat groups prefer to employ at least one sentinel the whole time can be confirmed. That is surprising because captive meerkat groups in enclosures have a very low predation risk relative to their free-living conspecifics (Clutton-Brock et al., 1999b). Nonetheless, captive meerkat groups also preferred having at least one guard most of the time to ensure safety – an inherent feature in both wild and captive meerkats.

One avenue of future research would be to investigate whether group size is the decisive aspect for the α-female to do guard work. In the present study, the α-female only was on guard duty in the little Vienna group. One potential conclusion is that in small groups the α-female's sense of responsibility increases, whereas in bigger groups there are enough subordinated individuals to do that job. This requires further investigations on captive and wild meerkat groups.

The enclosure might also influence sentinel behaviour in captive meerkats. Especially in enclosures with a separate inside and outside area, the animals have no reason to fear predators. Nonetheless, meerkats continue to show sentinel behaviour also in inside areas (Figure 1). This behaviour therefore seems to be a fixed behavioural pattern, independent of experience and effective predator stress. Therefore, the postulated hypothesis that sentinel behaviour is only shown in outside areas of the enclosures can be refuted.

Note here, however, that construction work in the open-air area in the Augsburg zoo during the first three days of observation might have influenced the group's inside/outside distribution. The utilization of open-air areas in zoos clearly also depends on the weather. Meerkats are naturally well-adapted to warm temperatures and dry regions (Müller & Lojewski, 1986a), so they shun cold temperatures. Extensive sunbaths to warm up the body take up a big part of a meerkat's day (Estes, 2012). Meerkats are entirely diurnal and the colder nights are spent in their burrows (Müller & Lojewski, 1986b). The Central European climate does not always match with the preferred weather conditions, so in winter, captive meerkats in our zoos visit the open-air areas more rarely than in summer. At cold temperatures, many group members move close together and build a cluster.

Group-living species such as meerkats that protect themselves by having sentinels prefer to stay in proximity (Gall & Manser, 2017) in order to better perceive the so-called 'watchman's song' that announces sentinel presence and informs group members that there is no current danger (Manser, 1999). The results of this study confirm this finding, demonstrating that group members maintained spatial proximity at all three locations. In Augsburg and Linz, the group sometimes split up to both parts of the enclosure (Figure 1). The small group in Vienna was always together, indicating that group size matters in terms of social cohesion. These observations support the theory on sentinel behaviour that captive behaviour does not differ from that in the wild: both stay close to the guard, especially when offspring are present. Therefore, the hypothesis that captive meerkat groups always try to stay in contact and in small distance to the current sentinel could be confirmed.

5.3 Response to bird calls

Various bird species are severe predators of wild meerkats and represent a constant threat from above. Not all species of predatory birds, however, pose equally strong threats. For this reason, meerkats have evolved various alarm calls that categorize such different danger levels (Dennis & MacDonald, 1999). Manser determined that sentinels always vary the alarm call patterns depending on the type of approaching predator (Manser, 1999)(Manser, Seyfarth, & Cheney, 2002).

The present investigation showed that meerkats distinguish very well between those bird species that represent a potential danger and those that do not. The playback experiments showed that meerkats can clearly distinguish the calls of predatory birds and songbirds. Songbird sounds were even ignored by the sentinel in some cases. In Augsburg, for example, the reactions to songbird calls were weak (Table 4) compared to predatory bird calls. Predatory bird calls were not ignored, with the sentinel showing various reactions to each of them such as ‘fast head movement’, ‘looking up to the sky’, ‘installation of additional guards’ and ‘pose changes’. At Linz zoo, the reactions to predatory bird calls were particularly intense. Importantly, the present study demonstrates that captive sentinels distinguish between different predator bird types as well. In the wild, meerkats have learned to categorize the risk of several predatory birds. Whereas some species pose a real danger for the whole group and escape is unavoidable, other species are lethal only for offspring (Dennis & MacDonald, 1999). The classification of threat levels is extremely important for the group, and the skill to do this reliably is a decisive requirement for a good sentinel. The group must be sure that the current sentinel is able to correctly assess the approaching enemy. Accordingly, the conclusion is that meerkats are mainly interested in those bird calls representing a potential danger for the group. The sentinels react more strongly only if they perceive large predatory birds, even in captivity.

Meerkat groups differ in their group composition regarding sex and age. A group’s reaction to external influences can therefore be influenced by group composition, for example the presence of offspring. The results of this study support that interpretation: the Augsburg group (with adults and a few cubs) reacted only slightly to songbird calls (Table 6) compared with the group in Linz (half of the group are cubs), which did react to songbird calls (Table 7). One potential explanation is that many sparrows live in the inside area (giraffe house) of the Augsburg enclosure. The constant exposure to sparrow calls no doubt involves habituation. The response to songbird calls by the group in Linz differed completely. The whole group showed more tension and alertness after hearing the played-back songbirds. One explanation is that the Linz group (made up by more than half of cubs) was more nervous. In the wild, meerkat groups and their sentinels are also much more attentive when offspring are part of the group and the cubs leave the protection of the burrow (Dennis & MacDonald, 1999). Alternative explanations are that the group in Linz generally had less experience with birds or that bad experiences in the past with birds made the group more sensitive.

The present results also indicate that habituation to certain bird calls could have influenced the reaction to the playbacks. When the group and their sentinels habituate to the sounds of specific bird species, such sounds are potentially classified as harmless and ignored.

Another interesting issue in the playback experiments was the question whether specific predatory bird species induce stronger reactions than others. The fact that meerkats can differentiate the threat levels of approaching enemies supports the assumption that experience and information about predators plays an important role. Meerkat alarm calls encode information that is motivational (level of urgency) and referential (predator specific) (Manser et al., 2002)(Hollén & Manser, 2006)(Townsend, Rasmussen, Clutton-Brock, & Manser, 2012). The structure of the alarm call also provides information about the distance and the direction of the incoming intruder (Manser et al., 2002). The closer the potential danger approaches, the more guttural the emitted alarm call. Whereas some predatory bird species are already announced at a great distance, other species are accepted within a shorter distance to the group before the sentinel reacts (Dennis & MacDonald, 1999).

My results showed that some bird species caused a much stronger reaction than others. The time the whole group needed to get back in a relaxed state after playing bird calls served as an indicator for the degree of fear. The meerkat groups in Augsburg and Linz showed long recovery periods after the calls of large predatory birds such as different eagle or buzzard species (Figure 14). Apparently, large raptors automatically induced stronger reactions in captive meerkats, although it is unlikely that these individuals have ever seen such a bird. Here, experience seems to play a lesser role, suggesting an imprinted knowledge about the danger. It is more likely that the meerkats can conclude from the detected calls how big the predatory bird and the upcoming threat level is. Wild meerkats also react differently to distinct raptor species. For example, eagle species such as the Tawny eagle (*Aquila rapax*) or Martial eagle (*Polemaetus bellicosus*) cause a long and aroused warning trill in meerkats because they represent a real danger. In contrast, other native predatory bird species like the White-backed vulture (*Gyps africanus*), Northern goshawk (*Accipiter gentilis*) or Bateleur

(*Terathopius ecaudatus*) that attack meerkats very rarely only induce short alarm calls (Dennis & MacDonald, 1999).

At the same time, past experience continued to influence the reaction to bird calls. This was indicated by the time the meerkat group in Linz needed to re-emerge from their burrows after an escape (Figure 15). The Common buzzard and Carrion crow induced the longest duration. Both are native species that occur regularly in Central Europe and overfly meerkat enclosures in zoos, representing a potential danger. The Linz zoo administration, for example, reported that, in the past, Carrion crows snapped meerkat pups. The group therefore had bad experiences in the past with these species. While other partially bigger raptors induced only short times to return, these two species extremely intimidated the meerkat group. This is strong evidence that individual experiences in the group also influence current reactions to different bird calls. In the wild, smaller predatory bird species are tolerated if they do not approach too closely. The alertness of meerkats and their sentinels increases during the time when the offspring leave the burrow: guaranteeing the safety of the pups is a key responsibility of sentinels (Dennis & MacDonald, 1999).

Overall, the present results reveal that captive meerkats react differently to different bird species. Experience and learning, beyond innate behaviour, seem to be important. Therefore, the hypotheses that captive meerkats show stronger reactions towards predatory bird calls and that some bird species induce stronger reactions could be confirmed. The assumption that captive meerkat groups differ in showing reactions towards bird calls could be also verified.

5.4 Further incidental observations

During data collection at the three zoos, certain incidental observations went beyond the study framework but are nonetheless of interest. In the Vienna zoo, a group of King Colobus monkeys (*Colobus polykomos*) live in socialization with the meerkat group. The Colobus monkey is a herbivorous, arboral species that eats mainly leaves, fruits and other plant food (Estes, 2012). Thus, there is no competition with meerkats concerning food, and the points of contact between the two species are infrequent. Nonetheless, by sharing the space, direct contact between the two species is inevitable and even desirable because socializations are increasingly being used in zoos to keep the animals busy like in their natural habitats. During the observation periods, the two species did not affect each other when a certain distance was maintained. Monkeys that were moving or climbing were watched by most of the meerkat group, and the whole group went away if the monkey came too close. Concerning the sentinel behaviour of the meerkat group, the current guard often interrupted its work when the monkey group or a solitary monkey approached. In most cases, however, the whole meerkat group changed its location and the sentinel took another guard position.

In the wild, meerkats usually live in close contact to other animal species. Abandoned and modified burrows of Cape ground squirrels (*Xerus inauris*) or Yellow mongooses (*Cynictis penicillata*) are frequently used as sleeping caves and escape possibilities (Meder, 1993). Sometimes, a burrow is shared with that species at the same time. In addition, meerkats react immediately to the alarm calls of the ground squirrel and vice versa (Dennis & MacDonald, 1999). Such a peaceful coexistence of meerkats and ground squirrels or yellow mongooses is only possible because there is no food competition between these species (Meder, 1993). A symbiosis with other animal species is not uncommon for meerkats, and socialization in zoos is a good strategy to simulate natural conditions in captivity as well.

Zoo animals are inevitably exposed to specific external influences because of the permanent contact with humans. As outlined above, meerkats know their predators exactly and captive meerkats therefore know that they have nothing to fear from humans. The habituation to certain noises and behavioural patterns of visitors is important for meerkats; most of the time, visitors are ignored by the animals. During my observation periods, visitors never noticeably affected the three investigated meerkat groups. Screaming children were ignored by the sentinels, as well knocking on the windows or taking photographs.

The animals did show some differences regarding the occurrence of vehicles in front of the enclosure or overflying planes and helicopters. Especially in Vienna, where the zoo is located directly in the flight lane of the Vienna International Airport, many aircraft crossed the grounds of 'Schönbrunn' during the whole day. The sentinels always looked up to the sky when planes approached, and their gaze followed them. This behaviour underlines that particularly objects from above are monitored closely by the sentinels to detect potential danger early on. The same behaviour was noticed in Linz when a helicopter flew over the enclosure. The whole group put their heads up and remained alert until the helicopter moved off. Captive meerkats seem to know that the only potential danger for the group is to be expected from above, and sentinels react much more strongly to detected objects or sounds in the sky.

Another observation was the influence of visitors with dogs, especially in Augsburg. Dogs are allowed in the Augsburg zoo, and the meerkat group often showed strong reactions after spotting them. As soon as a dog approached, the sentinel called out and the whole group looked up. Against expectation, however, the group organized itself and moved towards the dog. The adults lined up in front of the dog at the window and displayed defence behaviour. The same behaviour has been observed in the wild. Meerkats are very courageous animals that encounter certain predators with aggression. With good group organization and numerical superiority, enemies such as the Cape cobra (*Naja nivea*) and Cape fox (*Vulpes chama*) are attacked (Dennis & MacDonald, 1999). This highlights that meerkats are not naturally frightful animals simply because they try to detect potential danger early: they are quite capable of defending themselves against much bigger enemies.

6 Conclusion

This study provides first strong evidence that the sentinel behaviour of captive and free-ranging meerkats does not differ significantly. The natural behaviour including preferred lookouts from elevated spots, specific guard poses as well as individual preferences in working as sentinels or reacting to specific threats was documented.

The sentinel behaviour in meerkats involves various aspects of group life and social thinking, but selfish features also affect the individuals. Sentinels take on a responsible task to guarantee the safety of the whole group, regardless of whether they are in captivity or in the wild. The fact that ‘super sentinels’ were observed in all captive meerkat groups shows that communities clearly need individuals that assume this type of responsibility. Sentinels are exposed to increased predation risk and have less time for other activities. At the same time, however, there also enjoy beneficial aspects. A sentinel’s interests are promoted by the possibility to flee early in case of danger (based on the good outlook over the surroundings) and the chance to rise in the hierarchy. Moreover, the meerkats showed individual preferences in their guard behaviour concerning guard poses and guard positions, resulting in an individual ‘guard style’. Importantly, the groups had at least one sentinel on duty most of the time in order to minimize the period without guard (and the concomitant higher predation risk). The enclosure type did not seem to influence sentinel behaviour, which was displayed in both the inside and outside areas. Meerkat groups tried to stay together most of the time and maintained contact to the responsible guard to ensure safety.

The played-back bird calls also yielded new information. Captive meerkats were able to discriminate the calls of different species. Here, various aspects such as imprinted behaviour, experience and the presence of offspring play a role. The playbacks revealed that captive meerkats show behavioural patterns comparable to their conspecifics in the wild and that the group’s reaction depends on the detected predator type. Nevertheless, differences between meerkat groups were also observed: group composition and the individual characteristics of group members are apparently also decisive factors for the reactions.

Meerkats are intelligent animals with strong social behaviour and a high adaptability to their environment. The observation of the three zoo groups indicated that sentinel behaviour plays an extremely important role in the life of captive meerkats as well. The characteristic guard work goes beyond benefitting safety to take on a big part in meerkat social life. This investigation confirms that meerkats are important model organisms for biological research on a range of issues, but many riddles remain to be solved.

7 References

Clutton-Brock, T. (2002). Breeding together: Kin selection and mutualism in cooperative vertebrates. *Science*. https://doi.org/10.1126/science.296.5565.69

Clutton-Brock, T. H., Gaynor, D., McIlrath, G. M., Maccoll, A. D. C., Kansky, R., Chadwick, P., … Brotherton, P. N. M. (1999). Predation, group size and mortality in a cooperative mongoose, Suricata suricatta. *Journal of Animal Ecology*. https://doi.org/10.1046/j.1365-2656.1999.00317.x

Clutton-Brock, T. H., Maccoll, A., Chadwick, P., Gaynor, D., Kansky, R., & Skinner, J. D. (1999). Reproduction and survival of suricates (Suricata suricatta) in the southern Kalahari. *African Journal of Ecology*. https://doi.org/10.1046/j.1365-2028.1999.00160.x

Clutton-Brock, T. H., O'Riain, M. J., Brotherton, P. N. M., Gaynor, D., Kansky, R., Griffin, A. S., & Manser, M. (1999). Selfish sentinels in cooperative mammals. *Science*. https://doi.org/10.1126/science.284.5420.1640

Dantzer, B., Goncalves, I. B., Spence-Jones, H. C., Bennett, N. C., Heistermann, M., Ganswindt, A., … Clutton-Brock, T. H. (2017). The influence of stress hormones and aggression on cooperative behaviour in subordinate meerkats. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2017.1248

Dennis, N. & MacDonald, D. (1999). *Meerkats* (3rd Editio). London: New Holland Publishers.

Estes, R. D. (2012). *The Behaviour Guide To African Mammals* (20th Anniv). Berkeley, Los Angeles, London.

Ferguson, J. W. H. (1987). Vigilance Behaviour in White-browed Sparrow-weavers Plocepasser mahali. *Ethology*, *76*(3), 233. https://doi.org/10.1111/j.1439-0310.1987.tb00685.x

Gall, G. E. C., & Manser, M. B. (2017). Group cohesion in foraging meerkats: Follow the moving 'vocal hot spot.' *Royal Society Open Science*. https://doi.org/10.1098/rsos.170004

Hamilton, W. D. (1964). The genetical evolution of social behaviour. II. *Journal of Theoretical Biology*. https://doi.org/10.1016/0022-5193(64)90039-6

Hollén, L. I., & Manser, M. B. (2006). Ontogeny of alarm call responses in meerkats, Suricata suricatta: the roles of age, sex and nearby conspecifics. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2006.03.020

Hollén, L. I., & Manser, M. B. (2007). Persistence of alarm-call behaviour in the absence of predators: A comparison between wild and captive-born meerkats (Suricata suricatta). *Ethology*. https://doi.org/10.1111/j.1439-0310.2007.01409.x

Manser, M B. (1999). Response of foraging group members to sentinel calls in suricates, Suricata suricatta. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.1999.0737

Manser, M B, Bell, M. B., & Fletcher, L. B. (2001). The information that receivers extract from alarm calls in suricates. *Proceedings of the Royal Society B: Biological Sciences*. https://doi.org/10.1098/rspb.2001.1772

Manser, Marta B, & Bell, M. B. (2004). Spatial representation of shelter locations in meerkats, Suricata suricatta. *Animal Behaviour*. https://doi.org/10.1016/j.anbehav.2003.10.017

Manser, Marta B, Seyfarth, R. M., & Cheney, D. L. (2002). Suricate alarm calls signal predator class and urgency. *Trends in Cognitive Sciences*. https://doi.org/10.1016/S1364-6613(00)01840-4

Meder, A. (1993). *Lebendige Wildnis: Tiere der Wüste und Halbwüste*. Stuttgart: Verlag Das Beste.

Müller, E. F., & Lojewski, U. (1986a). Thermoregulation in the meerkat (Suricata suricatta schreber, 1776). *Comparative Biochemistry and Physiology -- Part A: Physiology*. https://doi.org/10.1016/0300-9629(86)90564-5

Müller, E. F., & Lojewski, U. (1986b). Thermoregulation in the meerkat (Suricata suricatta schreber, 1776). *Comparative Biochemistry and Physiology -- Part A: Physiology*. https://doi.org/10.1016/0300-9629(86)90564-5

O'Riain, M. J., Bennett, N. C., Brotherton, P. N. M., McIlrath, G., & Clutton-Brock, T. H. (2000). Reproductive suppression and inbreeding avoidance in wild populations of co-operatively breeding meerkats (Suricata suricatta). *Behavioral Ecology and Sociobiology*. https://doi.org/10.1007/s002650000249

Ridley, A. R., Raihani, N. J., & Bell, M. B. V. (2010). Experimental evidence that sentinel behaviour is affected by risk. *Biology Letters*. https://doi.org/10.1098/rsbl.2010.0023

Ridley, Amanda R., Nelson-Flower, M. J., & Thompson, A. M. (2013). Is sentinel behaviour safe? An experimental investigation. *Animal Behaviour*, *85*(1), 137–142. https://doi.org/10.1016/j.anbehav.2012.10.017

Ross-Gillespie, A., & Griffin, A. S. (2007). Meerkats. *Current Biology*. https://doi.org/10.1016/j.cub.2007.03.045

Scott, K. (2014). *Behaviour and Endocrinology of Meerkats in Zoos*. 188.

Tatalovic, M. (2008). Sentinels : meerkat superheroes. *Science in School*, (10).

Tatalovic, M. (2010). Evolution of raised guarding behavior in meerkats , Suricata suricatta. *The Journal of Young Investigators*, *19*(24).

Townsend, S. W., Rasmussen, M., Clutton-Brock, T., & Manser, M. B. (2012). Flexible alarm calling in meerkats: The role of the social environment and predation urgency. *Behavioral Ecology*. https://doi.org/10.1093/beheco/ars129

Von Staaden, M. (1994). Suricata suricatta. *Mammalian Species*.

Wilson, D. & Mittermeier, R. A. (2009). Handbook of the Mammals of the World Carnivores vol 1. In *Wilson DE Mittermeier RA Eds*.

Wilson, D. S., & Sober, E. (1998). Multilevel selection and the return of group-level functionalism. *Behavioral and Brain Sciences*, *21*(2), 305–306.

Zahavi, A. & Zahavi, A. (1997). *The Handicap Principle: a missing piece of Darwin's puzzle*. Oxford, New York: Oxford University Press.

Web addresses:

https://www.vogelstimmen.info/Vogelstimmen_Hoerproben_GRATIS.html, 03.10.18

https://www.iucnredlist.org/species/41624/45209377, 11.03.19

https://www.zoo-augsburg.de/erdmaennchenanlage/, 15.03.19

https://www.zoovienna.at/anlagen/historisches-affenhaus/, 15.03.19, Foto: Daniel Zupanc

Ich habe mich bemüht, sämtliche Inhaber der Bildrechte ausfindig zu machen und ihre Zustimmung zur Verwendung der Bilder in dieser Arbeit eingeholt. Sollte dennoch eine Urheberrechtsverletzung bekannt werden, ersuche ich um Meldung bei mir.

8 List of tables

9 List of figures

10 Attachment

10.1 Zusammenfassung

Erdmännchen sind für ihr ausgeprägtes Sozialleben und kooperatives Verhalten bekannt. Besonders der Wächterjob nimmt bei diesen Tieren eine verantwortungsvolle Aufgabe innerhalb der Gruppe ein. Daher stellt sich die Frage, ob bestimmte Individuen besser als Wächter geeignet sind als andere. Als Ziel dieser Arbeit sollte sowohl das individuelle Wächterverhalten als auch das der gesamten Gruppe im Detail untersucht werden. Dafür wurden Wachzeiten von Erdmännchen-Gruppen in drei verschiedenen Zoos aufgenommen und die Dauer der Einzelwachzeiten, die eingenommene Wächterhaltung, die Wachpositionen und in einem zweiten Teil die Reaktionen des Wächters und der Gruppe auf verschiedene Vogelstimmen genauer analysiert. Außerdem waren sowohl die Existenz von sogenannten „Superwächtern“ innerhalb der Gruppen als auch die individuellen Vorlieben verschiedener Wächter ein wichtiger Bestandteil dieser Untersuchung. Die Ergebnisse konnten bestätigen, dass einige Individuen den Wächterjob häufiger und effektiver durchführen als andere Gruppenmitglieder. Es konnte festgestellt werden, dass Wächter bestimmte Orte für ihre Arbeit vorziehen und es Unterschiede zwischen den Gruppen in Bezug auf die eingenommene Wachhaltung gab. Zusätzlich wurde deutlich, dass die Gruppen die meiste Zeit mindestens ein Tier als Wächter beschäftigten. Die Playback-Experimente in den jeweiligen Erdmännchen-Gruppen zeigten zum Teil große Unterschiede bei der Reaktion von Wächter und Gruppe auf bestimmte Greifvogel- und Singvogelarten. Das lässt den Schluss zu, dass Erdmännchen in der Lage sind, andere Arten als potenziell gefährlich oder harmlos einzustufen. Darüber hinaus wurden die erforderlichen Eigenschaften eines „guten“ Wächters und der Einfluss weiterer Parameter wie die Gruppengröße oder die Gehege-Anlagen der Zoos auf das Wächterverhalten diskutiert. Die Untersuchung zeigte, dass das Wachverhalten von Erdmännchen in Zoos sich nicht bedeutend vom Verhalten ihrer Verwandten in freier Wildbahn unterscheidet. Die Reaktion auf mögliche Fressfeinde hängt vielmehr vom Charakter des Wächters, Erfahrungen aus der Vergangenheit und dem Vorhandensein von Nachwuchs in der Gruppe ab.