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Sentinel behavior in captive meerkats (*Suricata suricatta*)

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Abstract

The social and cooperative behavior of meerkats (*Suricata suricatta*), specifically their sentinel behavior, has been intensively studied in free-ranging populations. This study focuses on whether guarding in captive meerkats exhibits a pattern similar to that described for wild groups. Sentinel behavior in captivity has been somewhat neglected because predation is usually not a critical factor. Nonetheless, observations in captivity might reveal whether individual or group experience influences this specific behavior pattern. We observed three captive meerkat groups (in outdoor as well as indoor enclosures) and analyzed the duration of guarding sequences, the number of established guards, the guard posture, and the individual guard positions. We also conducted playback experiments to investigate the reaction of the sentinel and the group to bird calls (songbird vs. predatory bird species). The results demonstrated that captive groups behave much the same as wild groups. Certain individuals performed the guard job more often than other group members. Accordingly, the "super sentinels" observed in the wild also exist in captive groups. Playbacks showed that the sentinels reacted more strongly to the calls of predatory bird species, indicating that captive meerkats are able to categorize bird calls. We also documented major differences in behavioral responses to the calls of specific predatory bird species. Our observations underline that sentinel behavior is probably a combination of an innate, imprinted pattern that is further affected by the experience. Future studies might further investigate this influence of experience, beyond innate behavior, on the group-specific sentinel behavior pattern in captive meerkats.

KEYWORDS

meerkats, playback experiments, predatory birds, sentinel behavior, "super sentinels"

1 | INTRODUCTION

In the animal kingdom, sentinel behavior, also known as guarding behavior, is a special form of altruism in cooperative societies (Ridley et al., 2010). Sentinel behavior has been described in various species, but is best known in mammals such as mongooses (Mulligan & Nellis, 1975; Manser et al., 2002; Rasa, 1985), ground squirrels (Hare, 1998; Sherman, 1985), and prairie dogs (Kiriazis & Slobodchikoff, 2006; Slobodchikoff & Coast, 1980). It has also been reported in different bird species such as the pied babbler (Ridley et al., 2010, 2013). A common assumption is that sentinel behavior provides benefits in terms of increased predator detection depending on group size, with smaller groups suffering higher mortality rates than larger groups (Clutton, Gaynor, et al., 1999). This makes the deployment of guards helpful and is often observed in animals that forage in groups. Sentinel behavior allows the individuals to reduce their own vigilance while maintaining the alertness of the group. This behavior is characterized by two main features: (1) certain individuals of the group scan for predators while the remaining members 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). With their characteristic and unique bipedal posture standing erect on the hind legs, meerkats (*Suricata suricatta*, Schreber et al., 1776) are one of the most popular examples for sentinel work.

Meerkats are often used as model organisms for altruistic behavior due to their cooperative breeding and feeding as well as community guarding. Meerkats fear various potential predatory species such as all larger terrestrial carnivores, but the avian threat is feared most. Healthy meerkat groups can compensate a certain mortality rate when the birth rate within the group is high enough to enable regeneration (Clutton-Brock, Gaynor, et al., 1999). Because they lack good running, climbing and jumping abilities and prefer open habitats, meerkats have evolved many antipredator strategies. These include the high-sit alert stance, flight to cover, defensive threat, mobbing attack, self-defense, and covering young (Estes, 2012), all of which help minimize the predation risk for the group (Dennis & MacDonald, 1999). Beyond sentinel work, alarm calling in meerkats plays an important role in predation avoidance. Vocalizations announce a potential danger outside the colony for the whole group (Moran, 1984). Moreover, variation in alarm calls provides information on the type of threat in a large number of animal species (Manser, 1999; Manser et al., 2002), for example on predator size (Templeton et al., 2005), distance (Manser et al., 2002), location (Cäsar et al., 2013), or the type and urgency of a flight response (Manser, 2001; Rauber & Manser, 2017).

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

The positioning of meerkat guards on elevated spots (Clutton-Brock, Maccoll, et al., 1999) and the specific calls for different predator classes (Manser et al., 2002) signal the approaching predator that it has been spotted. Moreover, meerkats always approach the nearest hideout when an alarm call is made, even if that specific threat is not yet visible, demonstrating their orientation and memory capability (Manser & Bell, 2004). Importantly, sentinel behavior may be beneficial to both the group and the guard itself. Zahavi and Zahavi (1997) suggested that a successful sentinel gains prestige and might increase its status within the group by demonstrating its quality as a mating partner or reliable group member. Finally, 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, O'Riain, et al., 1999).

Within wild meerkat groups, some individuals perform 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 (Tatalovic, 2008). Against expectation, super sentinels, however, are usually well-fed, indicating that they are effective foragers as well (Clutton-Brock, O'Riain, et al., 1999). The current hypothesis is that those meerkats that are highly efficient 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).

Whereas numerous studies have been carried out on the sentinel behavior in free-ranging meerkats (especially the research groups of Clutton-Brock and Manser), relatively little is known about that behavior in captive meerkats. Only Moran (1984) dealt extensively with vigilance behavior in captivity, investigating individual sentinel performance and alarm call characteristics in a small captive meerkat group. The present study builds on the findings of Moran by examining different captive groups in zoos in Austria and Germany. It also records the reactions of sentinels and groups to playback calls of different bird species to simulate predation events. This approach yielded further insights into whether sentinel behavior is an entirely innate behavior, or whether certain aspects are learned.

2 | METHODS

2.1 | Study sites

This study was conducted in three zoological institutions: Vienna zoo (Austria), Augsburg zoo (Germany), and Linz zoo (Austria). All enclosures were similarly structured with an inside and an outside area. The Vienna enclosure is completely behind glass and divided into three connected areas: the inside area (127 m^2) and two smaller "outside" areas of different sizes (93 and 49 m^2). The enclosure is integrated into the monkey house in the center of the zoo and the meerkat group is socialized with a group of King Colobus monkeys (*Colobus polykomos*). Nearby housed species are South American sea lions (*Otaria byronia*) and African penguins (*Spheniscus demersus*). At Augsburg zoo, the inside and outside areas are approximately the same size (inside: 30 m^2, outside: 40 m^2). Nearby housed species are Grévy's zebras (*Equus grevyi*) and Rothschild's giraffes (*Giraffa camelopardalis rothschildi*). At Linz zoo, the enclosure comprises a large outdoor area (121 m^2) and a small inside area (16 m^2). The meerkat enclosure has no other species housed directly nearby. The investigated meerkat groups differed in group composition and group size. The group in Vienna consisted of 6 individuals (2 adults, 1 subadult, 3 cubs), in Augsburg of 18 individuals (9 adults, 4 subadults, 5 cubs) and in Linz of 14 individuals (7 adults, 7 cubs). The average group size was 12.7 individuals per group. This study adopted the names of the individuals given by the zoos (Table 1).

2.2 | Data collection

Data were collected from October to December 2018 by recording at least 30 video hours per zoo to obtain an appropriate sampling size. A video camera (Nikon D5300) with two different lenses (AF-P NIKKOR

TABLE 1 List of individuals in each meerkat group with names, sex, age, birth year and birth location by facility

Facility	Name	Sex	Age (years)	Birth year	Birth location
Vienna zoo	Zuzu	f (α)	3	2015	Leipzig
	Chilili	m	5	2013	Vienna
	Akio	m	1	2017	Vienna
	Binta	f	1	2017	Vienna
	Bakadi	m	1	2017	Vienna
	Babu	m	1	2017	Vienna
Augsburg zoo	1	f (α)	9	2009	Erfurt
	2	m	6	2012	Augsburg
	3	m	4	2014	Augsburg
	4	m	4	2014	Augsburg
	5	m	4	2014	Augsburg
	6	m	4	2014	Augsburg
	7	m	3	2015	Augsburg
	8	m	2	2016	Augsburg
	9	m	2	2016	Augsburg
	10	f	1	2017	Augsburg
	11	f	1	2017	Augsburg
	12	f	1	2017	Augsburg
	13	f	1	2017	Augsburg
	14	f	0	2018	Augsburg
	15	f	0	2018	Augsburg
	16	m	0	2018	Augsburg
	17	m	0	2018	Augsburg
	18	m	0	2018	Augsburg
Linz zoo	Nadine	f (α)	6	2013	Linz
	Timo	m	8	2010	Linz
	Tulan	m	8	2010	Linz
	Tilda	m	8	2010	Linz
	Turbo	m	8	2010	Linz
	Tommy	m	9	2009	Linz
	Timon	m	9	2009	Linz
	-	f	0	2018	Linz
	-	f	0	2018	Linz
	-	f	0	2018	Linz
	-	f	0	2018	Linz
	-	m	0	2018	Linz
	-	m	0	2018	Linz
	-	f	0	2018	Linz

18–55 mm; AF-S NIKKOR 55–200 mm) was used to investigate the sentinel behavior patterns in detail and to identify the individuals. The playback experiment was conducted in Augsburg and Linz not in (Vienna was excluded because of its enclosure structure (completely behind glass) and because the meerkat group shared their space with a group of monkeys). The investigation was structured in two separate parts: (1) generally observing the sentinel behavior and the differences between the meerkat groups and (2) investigating the response of sentinels and groups to playbacks of different bird species.

The individual identification was based on the coloration and shape of the "eye masks." In addition to the black coloration, some animals also showed strongly contrasted stains with adjoining bright and dark colors around the eyes. In some cases, the coloration of the nose is useful because the black eye mask can reach the tip of the snout. In individual cases, morphological abnormalities such as a missing pinna, claws, or a shortened tail were helpful features.

For the first part of the study—general sentinel behavior—the focal animal (= the guarding individual) was used to record the duration of a guard sequence, the guard location, the number of current guards, and the associated guard pose. The group behavior during the sentinel sessions was also recorded with ad libitum sampling. A single observation session lasted 20 min. For each video the starting time was recorded along with the current location of the meerkat group in the enclosure. The number of current guards was also noted, including the times of guard-change. The focus, however, remained on the guard.

For the second part, playback experiments were conducted to investigate the behavior towards different bird sounds. The bird species were divided into two groups: songbird species and predatory bird species. The songbird group (8 species) was composed of native Central European species that are common in Austria and Germany. The predatory birds (12 species) encompassed a mixture of native Central European species as well as a few species that also inhabit southern Africa.

All observations were conducted in the indoor component of the enclosure because the meerkat groups stay inside most of the time in winter. Moreover, there were much fewer background noises in the inside enclosure, and the behavioral reactions could be definitively assigned to the playbacks. As in the first part, focal animal sampling was used to detect the behavior of the current sentinel and ad libitum sampling to record the group behavior. For precise documentation of the relevant behavior (Table 2), a suitable observation point with a view on all burrow entrances had to be chosen to record possible flight responses.

The duration of one playback sequence lasted 30 s. Each bird call was played back at least once in Linz and in Augsburg. Playback started when only a single individual was on guard position. The number of playbacks per day varied between 2 and 4 bird calls, depending on zoo activities. To avoid habituation to the playbacks, sound experiments were not run on consecutive days and a break of at least 1 h was taken in between the trials to

TABLE 2 Behavioral responses of the meerkat groups to the bird sounds in the playback experiment along with the definition of each described behavior pattern

Group reaction	Description
No reaction	Whole group shows no visible reaction to the bird sounds
Alerted	Some (or all) individuals raise their heads and show increased vigilance
Escape to the burrows	Some (or all) animals of the group escape to the burrows but do not hide
Escape in the burrows	Some (or all) animals of the group escape in the burrows and hide inside
Look out of the burrows	The hidden animals stick their heads out of the holes after flight response
Freezing behavior	The animals show no further movements and remain in place
Out of sight	No individual of the group is visible

ensure that the animals were in a calm state before the next playback started. The intervals between the playbacks were not fixed but adjusted to the current number of visitors at or near the enclosure and the presence of other background noises (delivery vans, cleaning activities, etc.). The audio level of all playbacks was controlled and exactly the same for all calls to avoid the influence of different volumes on the behavioral responses. A Telefunken BS1005M speaker (connected to a smartphone via Bluetooth) was used to play back the audio files (mp3). The speaker was concealed to ensure that the animals were unable to visually locate the sound source. Importantly, the speaker was not positioned near the observation spot to prevent the meerkats from making a connection between the observer and replayed sounds.

2.2.1 | Data analysis

Ethogram

Each sentinel behavior pattern within a video sequence was attributed to the corresponding behavioral category described in an ethogram (Table S1). The categories "guard number" and "guard pose" play an important role and are therefore briefly described in more detail here. A distinction is made between the number of guards, that is, one sentinel versus two and three sentinels to more than three individuals on sentry duty at the same time (community guarding).

Three different guard postures during sentry work were differentiated. The "Vigilance pose" (VI) describes the sentinel sitting on its backside with all four legs on the ground and slow head movement in all directions. In the "Guarding pose" (GUA), the sentinel sits on its hind legs, the upper body is upright, the front legs are docked to the body and frequent head movement is shown. The "Raised guarding pose" (RG) is the most noticeable posture: the sentinel stands on its hind legs (bipedal) and the body is completely outstretched. The guard often stands on its tiptoes, supported by the tail, and shows permanent head movement.

Video coding

Video coding (continuous recording) was done with the software "Solomon Coder" (version: beta 19.08.02). The duration of each sentinel behavior pattern was measured. The analysis function of the program supplied the duration (in seconds) and frequency of occurrence of the required information.

2.3 | Statistical analysis

For statistical analysis, the software Prism 8.0 (Graph Pad) was used, and the unpaired two-tailed Mann–Whitney *t* test (nonparametric) was applied with the same program. The level of significance was set to $\alpha = 5\%$.

3 | RESULTS

3.1 | General sentinel behavior

3.1.1 | Super sentinels

Describing the occurrence of "super sentinels" requires considering the differences in solitary guarding in each group. The guarding duration varied considerably between individuals (Figure 1). In Vienna, the young male "Akio" exhibited the highest proportion of single guarding time (70%), the other two individuals significantly less. Interestingly, the α female "Zuzu" also worked as a sentinel (20%). The cubs "Binta," "Bakadi," and "Babu" never served as solitary guards during the observation period. The percentage distribution of the Augsburg individuals shows that individual "no. 2" spent the most time single guarding (30%). Individual "no. 9" showed an only slightly lower value (29%). The rest of the group was rarely on guard duty. The α female ("no. 1") never served as a sentinel. In Linz, the values of single guarding time showed that mainly "Timo" (30%) and "Turbo" (32%) were on sentry duty. All other individuals worked considerably

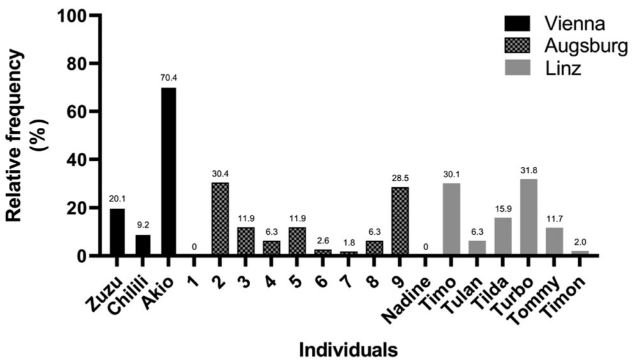

FIGURE 1 Percentage distribution of single guarding time for each individual in all three meerkat groups. Values indicate the sentry time of each individual in relation to the total observation time. Outliers were not removed from the calculations

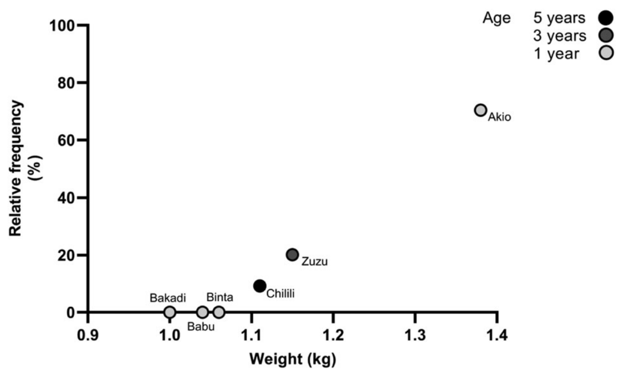

FIGURE 2 Percentage distribution in dependence of weight and age of the Vienna meerkat group. Values indicate the sentry time of each individual of the group in relation to the total observation time and the corresponding weight (representing foraging success). The respective age is also indicated

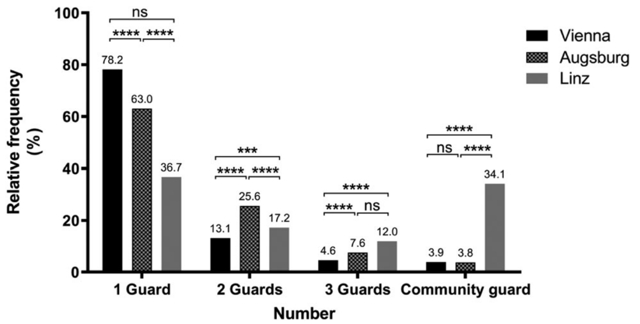

FIGURE 3 Distribution of the number of guards, directly comparing the percentage ratio of the number of guards for each zoo. Values indicate the sentry time with 1 guard, 2 guards, 3 guards, and community guarding for each meerkat group in relation to the total observation time. Statistical significance (MWU test): ****$p \le .0001$ (highest significance), ***$p \le .001$ (high significance), **$p \le .01$ (significance), $^{ns}p > .05$ (no significance)

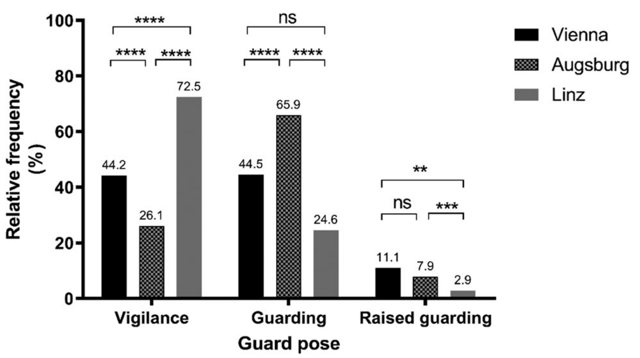

FIGURE 4 Distribution of the guard postures showing the percentage ratio of the poses taken during sentry duty in each meerkat group. Each group of three bars represents one posture, and the values indicate the sentry time in this certain pose in relation to the total observation time. Statistical significance (MWU-test): ****$p \le .0001$ (highest significance); ***$p \le .001$ (high significance); **$p \le .01$ (significance); $^{ns}p > .05$ (no significance)

shorter as sentinels. The α female "Nadine" spent no time as a sentinel.

The correlation between weight and sentinel behavior in the Vienna group (only the weight data of the Vienna group were available) demonstrated that the heaviest group member "Akio" (1.38 kg) also showed the highest percentage (70.4%) of sentinel behavior (Figure 2). The slightly lighter individuals "Zuzu" (1.15 kg) and "Chilili" (1.11 kg), however, showed significantly lower values (20.1% and 9.2%), and the three youngest and lightest individuals "Binta" (1.06 kg), "Bakadi" (1.00 kg), and "Babu" (1.04 kg) had no sentinel time.

3.1.2 | Group differences

The distribution of the number of guards (Figure 3) describes the differences in the number of established sentinels between the meerkat groups. The behavior pattern in Vienna (78%) and Augsburg (63%) was very similar (single guards most of the time): two or more simultaneous guards were rarely active, and community guarding was also rarely observed (< 4%). Interestingly, the Linz group showed a different sentry pattern. Community guarding (34%) was frequent and almost the same proportion as single guarding (37%). Two or three guards at the same time, however, were less common in all groups.

The guard pose distribution (Figure 4) describes the different sentinel poses during a guarding sequence (see ethogram section). The three groups exhibited major differences. The Vienna group showed the vigilance pose and the guarding pose in almost the same percentage (44%), whereas the raised guarding behavior was rare (11%). The Augsburg group exhibited the guarding pose two-thirds (66%) of the time. The vigilance pose value was 26%, whereas the raised guarding pose was low (8%). In Linz, yet another pattern emerged. There, the guard mostly took the vigilance pose (73%). The

TABLE 3 Results of the playback experiments at the Augsburg zoo and Linz zoo describing the group reaction to the different bird sounds. Separated into two categories (songbirds and predatory birds)

Group reaction								
Bird species		**No reaction**	**Alerted**	**Escape to the burrows**	**Escape in the burrows**	**Look out of the burrows**	**Freeze**	**Out of sight**
Songbirds	European tree sparrow	A	L		L	L		L
	European house sparrow	A L						
	European robin	A	L					
	Coal tit	A	L					
	Eurasian blue tit		A	L			A	
	Common blackbird	A			L			
	Eurasian wren	A	L	L				
	Common chiffchaff	A	L				L	
Predatory birds	White-tailed eagle		A				A	
	Steppe eagle		A L				L	
	Golden eagle		A L	A	L	L	A L	L
	Eastern imperial eagle		A L	L			A L	
	Short-toed snake eagle		A L	L			L	
	European honey buzzard		A	L				
	Long-legged buzzard		A L	L			L	
	Common buzzard		A		L	L		L
	Red kite		A		L		A	
	Northern goshawk		A	A	L	L	A L	
	Eurasian sparrowhawk		A L	L				
	Carrion crow[a]		A		L	L	A	

Note: A, occurrence at Augsburg zoo; L, occurrence at Linz zoo.

[a]Carrion crow included in predatory bird species because it poses a threat to meerkat cubs.

guarding pose made up 25% of the guarding time, while the raised guarding pose was very rare (3%).

3.2 | Response to playbacks of bird calls

Many different reactions of the sentinel and the group were recorded in this study (see Table 2 for descriptions of behavior patterns for group reactions). The group responses in Augsburg (Table 3) showed that seven out of eight songbird species did not induce a reaction (exception: Eurasian blue tit elicited "alerted" and "freeze"). In contrast, all predatory bird species induced a group reaction, the most frequent being "higher alertness" ($N = 12$) with elevated heads. The species that induced an "escape to the burrows" ($N = 2$) were the Golden eagle and Northern goshawk. Another frequent reaction to different predatory bird sounds was "freezing behavior" ($N = 6$). The Augsburg group showed no extreme reactions such as escape and hide in the burrows.

In Linz (Table 3), only the European house sparrow induced no reaction, whereas the other bird species stimulated different reactions, mainly "increased alertness" ($N = 11$) in response to songbird and predatory bird calls. Other more frequent reactions such as "escape towards the borrows" ($N = 7$), "escape into the burrows" ($N = 7$) and "looking out of the burrows" ($N = 5$) were induced by different playbacks (European tree sparrow, Eurasian blue tit, Common blackbird and Eurasian wren among the songbirds and Golden eagle, Eastern imperial eagle, Short-toed snake eagle, European honey buzzard, Long-legged buzzard, Common buzzard, Red kite, Northern goshawk, Eurasian sparrowhawk and Carrion crow among the predatory birds).

Overall, the meerkat group in Linz showed stronger reactions than the group in Augsburg. Considering the return time of the Linz group (Figure 5), the strongest reaction was in response to Common buzzard calls: the group fled into its burrows (consequently being out of sight), reappearing only after 41 min. The second strongest reaction was in response to Carrion crow calls: the meerkats returned after 14 min of hiding. The response to calls of the Golden Eagle, Red

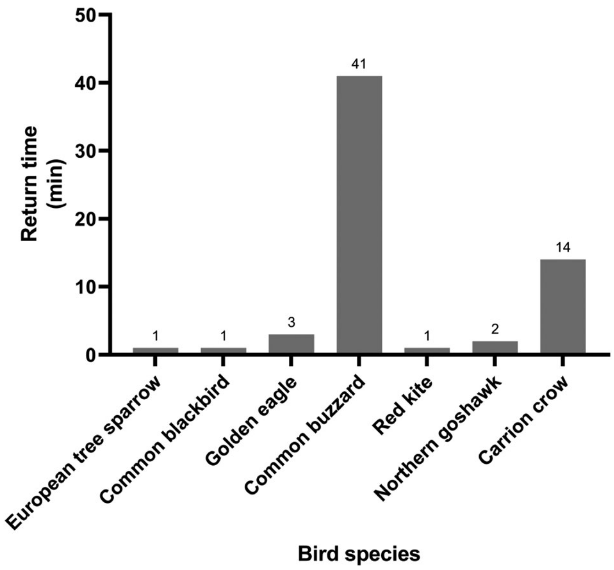

FIGURE 5 Return time of the Linz group: the time until the whole group in Linz re-emerged from its burrows after escape from the played-back bird calls. Only the bird species that induced a group escape are included. Rounded to full minutes

kite or Northern goshawk was also flight, but the group already reappeared after a few minutes.

4 | DISCUSSION

4.1 | Sentinel work

Meerkats must be highly attentive to avoid becoming victims of various predators in their natural habitat. Potential threats can occur at any time from every direction (Wilson & Mittermeier, 2009). Group survival therefore depends on installing sentinels. One might assume that more guards mean better protection, but that does not necessarily apply to meerkats. Moran's observations already revealed that one solitary meerkat took the sentinel position for a high proportion of time (Moran, 1984). The present results confirm this point, showing the presence of only one sentinel most of the time. In both Vienna and Augsburg zoos, the period with a single guard was high, underlining that the groups preferred this arrangement. The Linz group, by contrast, showed equal periods of time in single and community guarding, suggesting that different captive meerkat groups have distinct preferences regarding sentinel behavior. Group size and composition may be the decisive aspect and potential explanation for that. Studies in the wild showed that small groups suffer higher mortality rates and an increased threat of group extinction through droughts or predators (Clutton-Brock, Gaynor, et al., 1999; Rauber et al., 2019). With natural selection favoring larger over smaller groups, it makes sense for meerkats in the wild to have bigger group sizes with up to 30 individuals (Estes, 2012). Small groups naturally have fewer possibilities to exchange the sentinel, leading to more guard work with longer and more frequent periods for every individual per day. The observations on the small Vienna group confirmed that behavior pattern for captive meerkats. Nonetheless, the bigger Augsburg group's preference for one sentinel showed that this does not apply automatically. Group behavior, especially in captivity, can differ, and even bigger groups can tend to establish only one sentinel.

Scott determined that the blood cortisol concentration, as a hormonal stress response, was higher in captive meerkats kept in smaller groups (Scott, 2014; Scott et al., 2017). Furthermore, a recent study showed that stress hormones affect the cooperative behavior in subordinate wild meerkats (Dantzer et al., 2017). The dominant breeding pair and especially the dominant leading female puts pressure on subordinates and raises their stress hormone concentrations to boost the cooperative breeding and helping functions within the group (Carlson et al., 2004; Young et al., 2006). This is supported by Santema et al. (2013), who showed that glucocorticoids can affect foraging effort and affiliation with pups (albeit not cooperative behavior). The present study may support these observations because the dominant female showed no sentry time during the entire data collection in two of three groups (Augsburg and Linz). The α-females left the sentinel tasks entirely to the subordinate group members. Only the dominant female in the Vienna group took over sentinel tasks, but this can be explained by the small group size.

Different individual hormonal stress levels may also help explain the existence of so-called "super sentinels" (Tatalovic, 2008). The occurrence of these special individuals has been reported so far only in free-ranging meerkat groups (Clutton-Brock, O'Riain, et al., 1999). The present study, however, strongly indicates that "super sentinels" also exist in captivity. In all three zoos, specific individuals were on guard duty significantly more often and longer than other group members. As Moran (1984) proposed earlier, much evidence suggests that the sentinel behavior pattern is an integrated behavioral feature. But what drives this "hero behavior" in the safety of captivity?

One potential explanation is that certain individuals seek to gain status within the group by working as reliable guards. The sentinel can benefit by demonstrating its quality as a group member, mating partner or rival (Russell et al., 2003; 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.

Another finding in wild meerkat groups is that individual contributions to sentry duty vary widely and are positively associated with age, weight, and foraging success of the respective group member (Clutton-Brock, O'Riain, et al., 1999). Can this also be true of captive meerkats? The results of the Vienna group support the notion of a positive correlation between weight and frequency of sentinel behavior: the heaviest group member showed the highest level of sentinel behavior. This indicates that well-fed individuals may tend to perform the sentinels' job more often, even in captivity. Highly efficient foragers therefore seem to be more suitable "super sentinels" (Tatalovic, 2008). We were unable to confirm the positive effect of age because one of the youngest individuals served as sentinel most of the time. Note, however, that these results are based only on observations of a small meerkat group; more definitive conclusions would require further investigations.

An earlier study dealt with the individual consequences for the sentinel performing the sentry job and whether sentinel behavior is a special form of altruism or whether selfish and egoistic aspects play the decisive role (Clutton-Brock, O'Riain, et al., 1999). 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 been forwarded to explain this (presumable) altruistic behavior and the complexity of group life in meerkats. Previous studies also suggested that sentinels in wild groups suffer higher rates of predation than other group members (Ferguson, 1987; Rasa, 1986). This makes being a sentinel risky, and the more often an individual is on sentry duty, the higher its risk. The assumption was therefore that "super sentinel" meerkats accept this potentially increased risk. Later, more detailed investigations (Clutton-Brock, Gaynor, et al., 1999) found little evidence for such a higher predation risk: during the longer-term observations, no guards in raised pose were attacked or killed by predators. 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. Finally, sentinels are captured by terrestrial predators less often than other group members due to their elevated position and often closer distance to the burrow (Clutton-Brock, O'Riain, et al., 1999).

Concerning the selected guard posture, Moran (1984) determined that the sentinels behaved quite differently from the other group members. They showed an alert standing or sitting posture, whereas the other animals in the enclosure assumed these postures very rarely. But does sentinel performance also differ between meerkat groups?

Our study revealed such differences between the three investigated groups. Each showed a different pattern involving the three described poses "Vigilance," "Guarding," and "Raised guarding." One consideration is that the pose reflects the level of alertness during guard work. Experienced individuals tend to take a more relaxed pose (e.g., the vigilance pose) more quickly than inexperienced ones. This may help explain why younger group members rarely serve as sentinels (Dennis & MacDonald, 1999): they lack experience and might be less reliable. The quadrupedal vigilance posture seems to be the most relaxed guard pose, whereas the bipedal raised guard pose represents extreme alertness and tension (Moran, 1984). The most frequently observed pose in our study was "Guarding," which is intermediate between the other two.

On the individual level, we also detected some differences in the pose taken between group members. Certain individuals tended to use a preferred, favorite guarding pose, which was performed most of the time. In the Vienna group, the dominant female solely took on the quadrupedal vigilance pose, even in alert situations. Another younger male of the group, in contrast, mainly took on the guarding or raised guarding pose, never the more relaxed vigilance pose. This supports the hypothesis that each guard has individual preferences concerning location and pose.

4.2 | Predation response

Earlier studies already demonstrated that wild meerkats can categorize different danger levels. The established guards call out alarms specific to different types of approaching predators or intruders: avian predator, ground predator or a meerkat intruder (Manser et al., 2002). Meerkat alarm calls encode information that is motivational (level of urgency) and referential (predator specific) (Hollén & Manser, 2007; Manser et al., 2002; Townsend et al., 2012). That, however, raises the question whether captive meerkats can also differentiate between harmless and potentially dangerous predators despite the lack of experience.

Captive-born populations of meerkats use the same repertoire of alarm calls documented in wild populations in broadly similar contexts (Hollén & Manser, 2007; Moran, 1984). Accordingly, captivity and lack of experience do not influence such integrated, inherent antipredator behavior. Furthermore, captive meerkats can also discriminate between the feces of predators and non-predators, even without prior experience of predator odors (Hollén & Manser, 2007). These results suggest that captive meerkat populations perform correct antipredator behavior and that direct, physical interaction with predators is not a prerequisite.

Our playback experiments revealed that captive meerkats can discriminate the calls of predatory birds from those of songbirds. In all groups, songbird sounds were either ignored, or only low alertness was shown as the sentinel reaction (slightly increased vigilance but no flight response). Predatory bird calls, however, were not ignored and induced more intense behavioral responses. The sentinels showed various reactions such as fast head movement in all directions, pose changes or additional guard installation. Moreover, the group reactions were much stronger, showing flight responses, higher alertness or freezing behavior.

Importantly, reactions to certain predator types are not necessarily the same in different meerkat groups. One explanation is that meerkat groups differ in their group composition regarding sex and age (Estes, 2012). A group's reaction to external influences can therefore be influenced by group composition, for example by the presence of offspring (Clutton-Brock, Gaynor, et al., 1999; Townsend et al., 2012). The results of our study support that interpretation: the Augsburg group (only a few cubs) reacted only slightly to songbird calls, whereas the Linz group (half of the group were cubs) reacted more intensely and sensitively. The whole group seemed to be more alert and showed more tension after perceiving the played-back songbirds. In the wild, meerkat groups and their sentinels are also much more attentive when offspring are part of the group and when the cubs leave the protection of the burrow to discover their environment and forage with the group (Dennis & MacDonald, 1999; Santema & Clutton-Brock, 2013). Guaranteeing the safety of the pups is a key responsibility of sentinels (Dennis & MacDonald, 1999).

Another interesting aspect of the playback experiments is whether certain 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. This was supported by the lengthier time that the Linz group took to re-emerge from their burrows after a flight response. The Common buzzard and the Carrion crow induced the longest duration before the whole group re-emerged. Both bird species 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 Carrion crows have snapped and killed meerkat cubs in the past. This group of meerkats has therefore had previous deleterious interactions with this bird species, and the detection of Carrion crows leads to extensive alarm behavior. While other bigger raptors (without previous bad experience) induced only short times until return, these two species strongly intimidated the meerkats. This is compelling evidence that individual experience in the group also influences current reactions to different bird calls. In the wild, smaller predatory bird species are tolerated if they do not approach too closely. Some species are already announced at a great distance, other species are accepted within a shorter distance before the sentinel reacts (Dennis & MacDonald, 1999). Depending on predator type and the real danger exposure, the group must decide if a collective flight response is unavoidable or if only the offspring have to be protected. If hawks and eagles, the main enemies of wild meerkats, are sighted, constant vigilance and alarm calling are maintained. The entire group then typically flees for cover if an attack from above seems imminent (Estes, 2012).

Overall, our results revealed that meerkats show a pronounced sentinel behavior in captivity. We confirmed the hypothesis that predatory birds in general trigger stronger reactions of the sentinel and the group in captive meerkats as well. Furthermore, specific bird species induce much stronger behavioral responses than others, most likely due to previous experience and learning. Future studies might further pursue how big the role of experience, beyond innate behavior, is on the group-specific sentinel behavioral pattern.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

ETHICAL APPROVAL STATEMENT

The manager of the zoos issued permission for the research to be conducted. This study complies with all applicable Austrian laws and was conducted in accordance with the Guidelines for the Treatment of Animals in Behavioral Research and Teaching (ASAB, https://www.asab.org/ethics).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request. All data are already included in the manuscript.

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Additional Supporting Information may be found online in the supporting information tab for this article.

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